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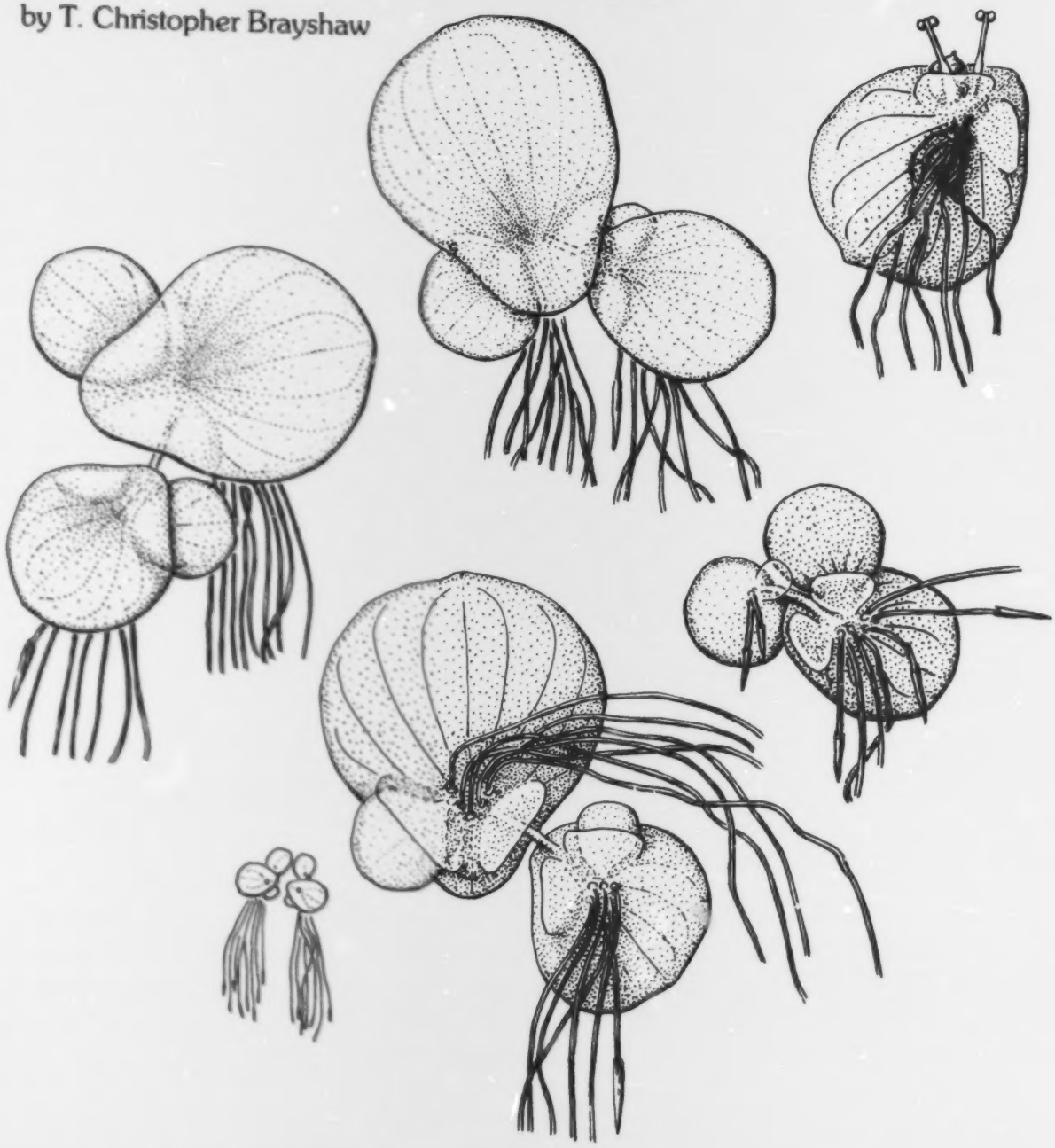
Pondweeds and Bur-reeds, and Their Relatives, of British Columbia

by T. Christopher Brayshaw



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Occasional Papers of the
British Columbia Provincial Museum
No. 26

Pondweeds and Bur-reeds, and Their Relatives: Aquatic Families of Monocotyledons in British Columbia

by

T. CHRISTOPHER BRAYSHAW

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PREFACE

For many years, while the terrestrial plants of the flora of British Columbia were becoming relatively well known, the aquatic members of the flora appeared to excite little interest. They were poorly represented in plant collections, and were correspondingly little known.

The past decade, however, has seen a rapid intensification of interest in aquatic plants. The principal reason for this increased interest is an ecological one. The progressive human impact on the waters and wetlands of this country has lately become sufficiently conspicuous to draw attention to the need for study and action. A knowledge of the indentities, distributions and abundances of the aquatic plants is one of the essential tools in assessing the effect of man's mainly terrestrial activities on the quality of the waters.

The six years during which this manuscript has been in preparation have seen a rapid information-growth that is still continuing. Extensive studies and collections have been made and analysed; and as a consequence our aquatic plant species are now becoming much better understood than they have ever previously been.

This publication deals with only a portion of the total number of our aquatic plant species. It is hoped that the remaining plants of wet habitats, mainly Dicotyledons, will be covered in subsequent publications.

In an effort to make this work widely usable, and at the risk of occasional lapses from absolute precision, the author has tried to avoid as much as possible the use of highly technical terminology, such as the highly specialized structures of these plants tend to demand. However, some use of technical terms is unavoidable. Therefore a glossary is included to explain the terms used.

The author would like gratefully to acknowledge the help of the staff of the British Columbia Provincial Museum, and the curators of other herbaria who made their collections available, and helped the author in his search for plant records. In particular the author is grateful to Drs. Adolph and Oldriska Ceska for much helpful discussion and information on some of our less well known species; and to Dr. A. Ceska and Dr. Robert T. Ogilvie for reviewing the manuscript.

T. C. Brayshaw
April 1981

ABBREVIATIONS AND SYMBOLS

cm centimetre.

comb. nov. new combination: indicating a change in combination of names without change in rank.

dm decimetre.

DC. De Candolle, Augustin Pyramus.

L. Linnaeus, Carolus (the elder).

m metre.

mm millimetre.

µm micrometre (1/1000 millimetre).

ssp. subspecies.

stat. nov. new status: indicating a change in rank in the hierarchy.

var. variety.

× hybrid: when used between specific names, implies a hybrid between them; when preceding a name, implies that the plant is a named hybrid.

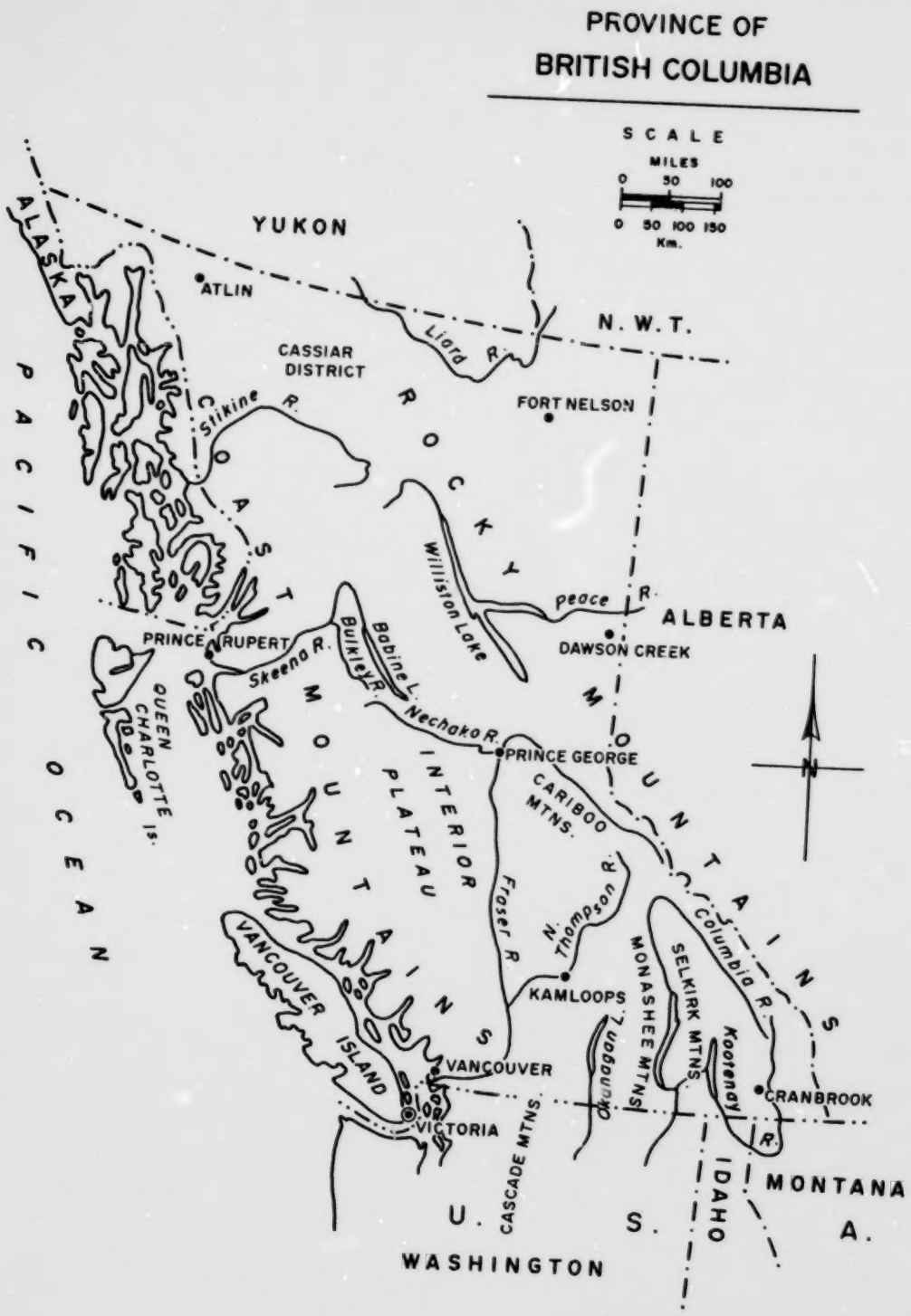
♂ staminate: the functional equivalent of 'male' in animals.

♀ pistillate: the functional equivalent of 'female' in animals.

± more or less, approximately.

CONTENTS

	Page
PREFACE	iii
ABBREVIATIONS AND SYMBOLS	iv
INTRODUCTION	1
Collections	1
Definition of the Group	1
CHECK-LIST OF FAMILIES, GENERA AND SPECIES	2
EXCLUDED SPECIES	4
THE AQUATIC ENVIRONMENT	4
General Types of Aquatic Vegetation	4
Community Succession	5
Aquatic Community Succession	5
Interactions Among Aquatic Plants	6
The Aquatic Environment as a Habitat for Plants	7
EVOLUTION IN AQUATIC PLANTS	8
Adaptations of Plants for Aquatic Life	8
Evolution and Classification of the Group	11
THE DIAGNOSTIC KEYS	11
Key to Families and Genera of Aquatic Plants in British Columbia	12
Key to Families and Genera Covered in this Work	18
DESCRIPTIONS OF FAMILIES, GENERA AND SPECIES	19
MAPS	129
GLOSSARY OF TERMS	123
BIBLIOGRAPHY	161
INDEX	164


PROVINCE OF
BRITISH COLUMBIA
SCALE
MILES
0 50 100
0 50 100 150
Km.
YUKON
ATLIN
ALASKA
N.W.T.
Liard R.
CASSIAR
DISTRICT
Stikine R.
FORT NELSON
ROCKY MOUNTAINS
COAST MOUNTAINS
Williston Lake
peace R.
ALBERTA
PRINCE RUPERT
Skeena R.
Bulkley R.
Babine L.
Nechako R.
DAWSON CREEK
PRINCE GEORGE
CARIBOO MTNS.
INTERIOR PLATEAU
Fraser R.
N. Thompson R.
Columbia R.
MONASHEE MTNS.
SELKIRK MTNS.
KAMLOOPS
Okanagan L.
Kootenay R.
CRANBROOK
VANCOUVER
VICTORIA
VANCOUVER ISLAND
CASCADE MTNS.
QUEEN CHARLOTTE IS.
PACIFIC OCEAN
U. S. A.
WASHINGTON
IDAHO
MONTANA

INTRODUCTION

Collections

Aquatic plant species are seldom as well represented in herbaria as are terrestrial plants. Among the reasons for this situation are the unobtrusiveness of many of the submerged plants, that are concealed out of sight from an observer standing on dry land, the necessity of having a boat for adequate sampling of open-water plant communities, and the awkwardness and discomfort that discourage people from sampling swampy or marshy vegetation types. As a result, few collections of many of our aquatic species have been made, and our knowledge of our aquatic flora is correspondingly weak.

In an attempt to fill in the gaps in our knowledge of these plants the author has taken a boat or canoe in the field during the past few summers, and concentrated on collecting from aquatic sites distributed widely across British Columbia. The resulting collections are filed in the herbarium of the British Columbia Provincial Museum, in Victoria, B.C.

In addition to these collections, aquatic plant collections made in this province have been examined in herbaria at the University of Victoria, at the University of British Columbia, at Vancouver, and at the National Museum of Natural Sciences and the Biosystematics Research Institute of Agriculture Canada, at Ottawa, as well as in the herbarium of the British Columbia Provincial Museum.

This work is primarily taxonomic and descriptive in scope, and treats the aquatic families of one class of flowering plants: the Monocotyledons.

Among the Dicotyledons, aquatic species and genera are scattered through a large number of families, few of which are completely aquatic. On the other hand, the aquatic species of Monocotyledons are more confined to a number of families that, in British Columbia at least, are completely and characteristically aquatic.

Definition of the Group

The plants described in this paper form a somewhat heterogeneous assembly of several rather small orders and families of the Class Monocotyledonae (the Monocotyledons), all of whose British Columbia representatives are aquatic to varying degrees. All the members of these families here are herbaceous, and show various kinds and degrees of modification for life in aquatic environments. Otherwise, while often sharing few conspicuous physical features in common, they may indicate their relationships in anatomical details often of microscopic scale.

It is generally agreed that this group includes, in the Helobiae, the most primitive members of the class. This is indicated by a number of features of structure and development in which they resemble primitive Dicotyledons. These features include the occurrence of such primitive characteristics as separate carpels, often of indefinite number, in the flowers, and the non-coherent margins of the carpels in some species. Even the great plasticity of form is itself a reflection of a lack of advanced specializations in the ancestral founding stock, while at the same time it is a character of positive value for facilitating adaptations to a variety of aquatic environments. The absence from most of these plants, except in the roots, of the tubular vessels (trachiae) that characterize the water-conducting system of most Dicotyledons, may be a secondary reduction associated with an early phase of partial aquatic adaptation by the ancestors of this class.

The classification system used in this work is only one of several that have been proposed. No system proposed to date has gained universal acceptance as a natural scheme. Other, more natural systems, better reflecting the true relations among these plants, will undoubtedly appear in the future, as active research currently under way improves our knowledge of these interesting plants.

As treated here, these plants are grouped into 14 families in four orders, as follows:

1. The Order Helobiae (Alismatales or Najadales), a complex order containing eight families here, of very diverse aspect, have little that obviously relates them together except for the absence of endosperm in the mature seeds, the usually coiled or horseshoe-shaped embryo, the presence of minute axillary scales ('*squamulae intra-vaginales*') in the axils of the leaves (and difficult to see), and their universally aquatic habit.
2. The Order Farinosae are distinguished by seeds with a starchy or floury endosperm and a straight embyro, and the carpels united into a superior ovary, forming a capsule with several seeds or a one-seeded utricle. An order of 13 small to medium-sized, mainly tropical, families, only one of which, the Pontederiaceae (Pickerel weed Family) is represented here.

3. The Order Arales (Spadiciflorae or Spathiflorae) have seeds usually with fleshy endosperm and a straight embryo, axillary scales in some, bundles ('raphides') of calcium oxalate crystals in some of the cells of most species, and an ovary composed of carpels that are coherent if more than one. Two families: the Araceae (Arum Family) and Lemnaceae (Duck weeds).

4. The Order Typhales have vessels in all their vascular tissues, and unisexual flowers in very dense spikes or heads, the staminate spikes or heads above the pistillate ones on the same shoot; with scale-like or bristle-like tepals, and seeds with endosperm. Both of the component families, the Typhaceae (Cat-tails) and Sparganiaceae (Bur-reeds), are represented in British Columbia.

A check-list of the species covered here, in their families and orders, follows.

Four families of Monocotyledons that contain some aquatic species, are omitted here. These are: The Gramineae (Grasses; of the Order Graminales), Cyperaceae (Sedge Family; Order Cyperales), Juncaceae (Rushes; Order Liliiflorae), and Iridaceae (Iris Family; Order Liliiflorae). The Grasses and Sedges are subjects of separate handbooks, the Rushes of British Columbia need further work, and probably should be the subject of a separate handbook, and the Irises are mostly terrestrial, with two aquatic species in British Columbia, *Sisyrinchium californicum* and the introduced *Iris pseudacorus*.

CHECK-LIST OF THE AQUATIC MONOCOTYLEDONOUS FAMILIES TREATED IN THIS WORK

Order **HELOBIAE (NAJADALES)**

Family BUTOMACEAE
- *Butomus umbellatus* L.

HYDROCHARITACEAE
- *Elodea canadensis* Richard
- *E. densa* (Planchon) Caspary
- *E. nuttallii* (Planchon) St. John
- *Vallisneria americana* Michaux

SCHEUCHZERIACEAE
- *Scheuchzeria palustris* L. var. *americana* Fernald

ZOSTERACEAE
- *Phyllospadix scouleri* Hooker
- *P. serrulatus* Ruprecht
- *P. torreyi* Watson
- *Zostera japonica* Ascherson and Graebner
- *Z. marina* L.
  - var. *latifolia* Morong
  - var. *marina*
  - var. *stenophylla* (Rafinesque) Ascherson and Graebner

ALISMATACEAE (ALISMACEAE)
- *Alisma gramineum* Gmelin
  - var. *angustissimum* (DC.) Hendricks
  - var. *gramineum*
- *A. plantago-aquatica* L.
- *Sagittaria cuneata* Sheldon
- *S. latifolia* Willdenow

JUNCAGINACEAE
- *Lilaea scilloides* (Poiret) Haumann
- *Triglochin concinnum* Davy
- *T. maritimum* L.
- *T. palustre* L.

POTAMOGETONACEAE
Potamogeton alpinus Balbis
var. *subellipticus* (Fernald) Ogden
var. *tenuifolius* (Rafinesque) Ogden
P. amplifolius Tuckerman
P. crispus L.
P. diversifolius Rafinesque
P. epihydrus Rafinesque
var. *epihydrus*
var. *ramosus* (Peck) House
P. filiformis Persoon
P. foliosus Rafinesque
var. *foliosus*
var. *macellus* Fernald
P. friesii Ruprecht
P. gramineus L.
var. *gramineus*
var. *maximus* Morong
var. *myriophyllus* Robbins
P. illinoensis Morong
P. natans L.
P. nodosus Poiret
P. oakesianus Robbins
P. obtusifolius Mertens and Koch
P. pectinatus L.
P. perfoliatus L.
ssp. *perfoliatus*
ssp. *richardsonii* (Bennett) Hulten
P. praelongus Wulfen
P. pusillus L.
var. *pusillus*
var. *tenuissinus* Mertens and Koch
P. robbinsii Oakes
P. strictifolius Bennett
P. vaginatus Turczaninow
P. zosteriformis Fernald
Ruppia maritima L.
var. *longipes* Hagstroem
var. *maritima*
var. *occidentalis* (Watson) Graebner
var. *spiralis* (Dumortier) Moris
ZANNICHELLIACEAE
Zannichellia palustris L.
NAJADACEAE
Najas flexilis (Willdenow) Rostkovius and Schmidt

Order **FARINOSAE**
Family PONTEDERIACEAE
Heteranthera dubia (Jacquin) MacMillan
Pontederia cordata L.

Order **ARALES (SPADICIFLORAE, SPATHIFLORAE)**
Family ARACEAE
Acorus calamus L.
Calla palustris L.
forma *palustris*
forma *polyspathacea* Victorin and Rousseau
Lysichiton americanum Hulten and St. John

LEMNACEAE
Lemna minor L.
L. trisulca L.
Spirodela polyrhiza (L.) Schleiden
Wolffia borealis (Engelmann) Landolt and Wildi

Order **TYPHALES**

Family TYPHACEAE
Typha latifolia L.
forma *latifolia*
forma ambigua (Sonder) Kronfeld

SPARGANIACEAE
Sparganium americanum Nuttall
S. angustifolium Michaux
ssp. *angustifolium*
ssp. *emersum* (Rehmann) Brayshaw *stat. nov.*
var. *chlorocarpum* (Rydberg) Brayshaw *stat. nov.*
var. *emersum*
var. *multipedunculatum* (Morong) Brayshaw *stat. nov.*
S. eurycarpum Engelmann
var. *eurycarpum*
var. *greenei* (Morong) Graebner
S. fluctuans (Morong) Robinson
S. glomeratum Laestadius
S. hyperboreum (Hartmann) Fries
S. minimum (Hartmann) Fries

EXCLUDED SPECIES

***Typha angustifolia* L.**

T. angustifolia has relatively slender leaves and spikes, the staminate and pistillate spikes separated by a bare stem-segment, minute linear bracts with dilated tips interspersed among the pistillate flowers, which have linear, projecting stigmas, and pollen shed in single grains, not in tetrads.

This species is reported in literature as occurring in British Columbia but no material definitely identifiable as this species has been seen by the author. *T. latifolia* forma *ambigua*, with its often relatively slender staminate and pistillate spikes separated by a bare segment of the stem, resembles *T. angustifolia* in gross appearance, and may be mistaken for this species being identifiable correctly and unquestionably only with the aid of a microscope.

***Vallisneria spiralis* L.**

This plant is suspected of having been introduced from Europe. Pistillate material is often difficult to distinguish from that of *V. americana* and some of it has been identified as that species. However, staminate flowers are more readily distinguishable. All staminate flowers seen by the author have been of *V. americana*, and it is presumed that all pistillate plants are of the same species.

THE AQUATIC ENVIRONMENT

General Types of Aquatic Vegetation

There is a rich diversity of aquatic habitats in British Columbia and their classification is beset with unresolved complexities. Even circumscribing the application of the term 'aquatic' can be the subject of debate, and is, in the end, decided arbitrarily. Generally, the term may be applied to habitats having a permanent water surface, or subject to seasonal flooding or saturation.

Quite apart from the broad regional diversity, with its corresponding diversity of macroclimates, there are varied local wet habitats conditioned by topographic situation, fresh-water or marine environment, type and speed of water movement, salinity, acidity, nutrient availability, etc.

There are continuous gradients in the determining factors by which the habitats intergrade with each other and with terrestrial habitats. Thus, a certain degree of arbitrariness must be assumed in drawing up any scheme for their classification.

The following general classification is simplified from Zoltai (1976).

1. Open Water
2. Bog
3. Swamp
4. Fen
5. Marsh

1. Zoltai classes as *Open Water* any area of which more than 75% is covered by open water. He also sets a depth limit of two metres but, since many aquatic plants have their bases more than two metres below the water surface, this seems an unnecessary restriction.
2. A *Bog* is a spongy mossy formation usually dominated by species of *Sphagnum* moss. The water typically is held in the moss, is acid, and is low in available nutrients. The underlying mineral soil is inaccessible to the roots of plants. Crowberry, ericaceous (Heath Family) shrubs, sedges, and insectivorous plants are characteristically present; and trees, such as black spruce and tamarack, may be present as open stands of small stature.
3. A *Swamp* is a wooded wetland that is not highly acid or dominated by *Sphagnum* moss. Commonly bordering lakes or streams, it may be dominated by trees or by tall shrubs, such as willows, alders, or shrubby birches.
4. A *Fen* is an open wetland with a consolidated surface, dominated by sedges or grasses; often with linear patterns of sparse shrubs or trees, and drainage channels and ponds.
5. A *Marsh* is an open, treeless site with an unconsolidated surface, and with a herbaceous cover of grasses, sedges, bullrushes, cat-tails, or other plants, often in clumps among drainage channels and ponds. This class includes the tidal marshes of the sea coast, as well as fresh-water marshes.

All these classes of wetlands can be further subdivided according to local situations or conditions.

Community Succession

In water, as on land, nothing is permanent, nothing is static. All natural communities undergo changes in the course of years, centuries, or millennia. As environmental conditions at a site change, through geologic or prolonged climatic changes, or through changes induced by the plants themselves, the species initially occupying the site are replaced by others that are better adjusted to the altered conditions. The process continues until the first community has been completely succeeded by another. This process is known as succession.

The succession that follows the usually slow and irreversible geological processes of weathering, erosion, and deposition, is termed Primary Succession. Superimposed on the primary successional trends are short-term, often cyclic, modifications caused by incidental, temporary disturbances such as flooding, fires, land clearing, or other human activities. Such changes, which are normally reversible, and often rapid, are termed Secondary Succession.

A community reacts upon itself by moderating the basic physical conditions, such as through the provision of shade and shelter and the deposition of litter by the dominant plants. This affects the selection of succeeding species, and is often an important factor in determining successional trends, especially in secondary succession.

Aquatic Community Succession

It is widely understood that a lake is a trap for sediment carried into it from surrounding land. Deposition of inorganic silt may be supplemented by that of organic debris where, in an oxygen-deficient environment, organic material can accumulate faster than it decomposes. In this way a lake becomes shallower until eventually the solid bottom lies exposed to the air. At successive stages in this physical process, successive communities of plants, each adapted to a certain range of water depth, occupy a site, until open water communities give way to marsh, fen, or swamp communities.

Succession in the opposite direction may also occur in cold regions. Where soil drainage becomes impeded, specially in areas of low relief, the water-table rises to the surface, and peat-mosses (*Sphagnum* spp.) assume dominance of the saturated site. The slow oxidation of their remains under these conditions leads to the accumulation of peat, and the eventual replacement of the forest cover by a boggy landscape of peatlands and ponds.

Lakes and streams in settled districts are inevitably affected by human activities, and secondary successional changes are extensively altering the primary succession of natural communities. A type of secondary succession that is becoming ever more remarked on is that caused by pollution of waters by material of terrestrial origin. The addition of nutrients in solution or suspension, including nitrogenous substances and phosphates, from sewage, or from fertilizer-laden runoff from cultivated land, alter the chemical nature of the aquatic environment. This provides special favours for those species that can take advantage of the nutrients and indulge in excessively vigorous growth at the expense of those species that are unable to benefit from the enriched environment. By the shading or crowding out of the latter by the former, a new community is selected out of the former one, and the slow succession of the original aquatic communities accelerates in a new and often unpredictable direction.

One consequence of the relatively heavy reliance by aquatic plants on vegetative reproduction compared to sexual reproduction is the frequent occurrence of extensive clones—dense colonies of genetically identical "individuals". A colony of a species of this kind, once firmly established, may dominate an area to the almost complete exclusion of other potential competitors, and continue to dominate long past the point of the species' optimum adjustment. Under these conditions, invading members of a later succeeding stage must not only be adapted to the changing physical environment, but must be able to compete with the old established clones of earlier successional species. This condition undoubtedly has a restraining influence on the rate of community succession.

Interactions Among Aquatic Plants

The interactions among members of aquatic communities are often very complex. Competition for light, oxygen, and dissolved nutrients play an important part. Competition for light, with its secondary effects on oxygen availability and temperature gradients, is the most easily visualized.

Although deeply submersed plants may obtain sufficient light for photosynthesis in clear water, the growth of densely leafy plants with foliage at or near the water surface, often accompanied by growths of suspended or attached algal colonies, can drastically reduce the amount of light reaching plants at greater depths. The effect is analogous to that in a deep forest, where the lower strata of a multi-layered community must tolerate the deep shade cast by the tall, canopy-forming trees.

Plants with broad floating or emergent leaves are usually confined to sheltered bays and ponds, since they are mechanically ill-adapted to withstand the impact of heavy wave action. Where they occur, however, they may so shade the underlying water that very little in the way of submersed plant life can grow beneath them and submersed species tend to be poorly represented. The latter, however, may be well represented in waters that are too deep or exposed to be dominated by the floating leaf forms.

As a secondary effect, the reduced light intensity in deep water results in a reduced rate of photosynthesis and oxygen production by deeply submersed foliage. This can lead to oxygen-deficiency, since no surplus oxygen is produced there beyond what the lower parts of the plants demand at night, while much of the surplus oxygen produced by floating and emergent leaves is passed directly to the atmosphere. Direct solution of atmospheric oxygen in the water is inhibited where the surface is covered by floating leaves.

An oxygen shortage at depth can affect animal life not only directly, but indirectly, through the induction of anaerobic decay of organic detritus the presence of which induces an oxygen demand in excess of the available supply. Such a situation becomes habitable only for anaerobic bacteria, with the consequence of the production of methane, hydrogen sulphide, and possibly even more toxic metabolic end-products.

By inhibiting the penetration of sunlight to deep waters and obstructing water circulation, the presence of a wealth of foliage at or near the surface leads to exaggerated temperature differences with depth, and enhances the normal stratification of the water. Surface water becomes very warm, while vertical mixing of this with the cool bottom water is impeded, and the bottom remains cool (Dale and Gillespie, 1977).

Though interactions with animals are hardly within the intended scope of this work, it should be pointed out that many of the plants dealt with here are important food sources for waterfowl and aquatic rodents such as muskrats (Fassett, 1940). Waterfowl are important dispersing agents for many of these species.

The Aquatic Environment as a Habitat for Plants

The management of its water resource is a problem encountered by every plant on land. Water must be obtained from an often irregular source of supply, and then conserved against excessive loss by evaporation. The need to facilitate the exchange of oxygen and carbon dioxide between the internal tissues and the atmosphere imposes a need for mechanisms that compromise the retention of water against evaporative loss.

The aquatic habit, with the roots, and often the entire plant, immersed in water, relieves the plant of the problem of maintaining the resource of which it is in the most constant need. However, relief from this stress is obtained only at a price. The abundance of water is associated with several other kinds of stress or hazard to which land plants are not exposed, but to which plants must evolve adaptations if they are successfully to exploit a watery environment.

The special environmental factors presented by a fully aquatic habitat include the following:

1. *Mechanical*

Water provides support through buoyancy, making sturdy, rigid stems and woody tissue unnecessary.

Water movement, by river currents, tidal currents, or wave action, may buckle or break stems of the rigidity required by upstanding land plants; making stiff or woody tissues an actual disadvantage.

The abrasion of foliage and stems against rocks by heavy wave action makes necessary the continual replacement of the lost tissues by some mechanism that is not itself exposed to the abrasion.

2. *Gas Exchange*

Oxygen and carbon dioxide are but moderately soluble in water, and diffuse much more slowly in water than in air. There is therefore a serious problem associated with the need to supply oxygen to, and remove carbon dioxide from, rhizomes and roots that are buried in unaerated mud at the bottom of a water body, or merely deeply submerged where the water is stagnant. Even in marshes or fens, water-saturated, unaerated soil inhibits the diffusion of oxygen to buried roots except via the plant's internal air passages.

3. *Opacity of Water*

Though intrinsically transparent, water often carries material in solution or suspension that absorbs the incoming light, so that insufficient light reaches the bottom in deep water to support plant growth. Waters of this kind, as in many of our silt-laden streams, are usually sterile of vegetation, except where very shallow.

4. *Fluctuating Water Levels*

The unreliability of the main resource—water—is emphasized in the alternate flood and drought that affects water bodies, such as reservoirs with deep seasonal draw-downs, or rivers such as the Fraser, where the winter low water level (when the water is clear) exposes to drought and frost plants that are submerged during the summer growing season to depths at the limit of light penetration through the now turbid water. Such a situation is practically impossible for any flowering plant to invade and is inhabited, if at all, only by a few lichens or mosses.

5. *Interference with the 'Traditional' Pollination Systems*

Primitively, flowering plants are pollinated by insects; wind-pollination is the commonly seen response to situations in which insects are less effective than wind. Progressively more extreme aquatic environments pose progressively more intense interference with the pollinating systems dependent on insects.

Flooding or frequently repeated inundation by waves or tidal action can render the normal pollinating vectors of terrestrial plants with aerial flowers—insects, or even wind—inoperative or at least inefficient. Invasion of aquatic environments thus requires plants to develop adaptations of their pollinating systems to this special situation.

6. *Seed Dispersal and Reproduction*

The pick-up of wind-borne fruits or seeds from a water surface by wind would be risky, and the distance conveyed short. Thus we see few wind-borne fruits or seeds in aquatic plants; the notable exception in this group being *Typha*, which carries its fruiting spikes usually a metre or more above the water. Dispersal by land birds is likewise hindered, since they require perching places adjacent to

their food: something that is commonly lacking in extreme aquatic situations. In fact we see few aquatic plants producing berries that would be attractive to land birds; *Calla* is an exception, which normally grows attached to the shore, or among emergent shrubs, and holds its fruiting spike above the water. The different foraging habits of aquatic birds and mammals impose different systems of growth and reproduction on the plants that exploit them.

EVOLUTION IN AQUATIC PLANTS

Adaptations of Plants for Aquatic Life

The aquatic plants treated herein display a fascinating diversity of modifications that adapt them to their environment. Starting from an original more or less terrestrial plant with erect form and complete, showy flowers pollinated by insects (the basic pattern in flowering plants), progressive modifications may involve any one or more of the following changes:

1. *Conservation of Supporting Tissue*

In a fully aquatic environment, significant material and synthetic effort can be conserved through the reduction or loss of woody vascular tissue (xylem). The xylem's rigid, supporting function is replaced by the buoyancy of the water, and, apart from the secondary function of transporting absorbed nutrients about the plant, its water-conducting function is superfluous to a plant that is immersed in water. Stiffening by lignification of such xylem cells as remain may be reduced or even eliminated.

2. *Attainment of Flexible Strength*

The development of long pliable stems or leaves enables plants to bend to water currents without breaking. This is largely achieved through the concentration of the vascular tissues of a stem into a slender, central, poorly lignified strand, having tensile strength but no rigidity. Where extra tensile strength is then needed, as in the surf-grasses (*Phyllospadix*), the vascular strands are supplemented by numerous very fine strands of sclerenchyma, whose thickened cell walls provide strength without a conducting function. An important aspect of growth here lies in the activity of basal meristems: special growing tissues, widely found in Monocotyledons, at the bases of internodes of stems and at the bases of leaf blades. These meristems produce new stem or leaf tissues, facilitating the elongation of stems and the replacement of leaves from the bases as the tips are abraded away by water movement.

3. *Development and Function of Lacunate Tissue*

Lacunate Tissue: spongy tissue containing interconnecting air-passages (lacunae); may serve two purposes: (a) for buoyancy; to maintain foliage near or at the surface of the water, or to hold an inflorescence above the water; or (b) to improve gas-exchange in deep-lying tissues allowing oxygen to reach buried rhizomes and roots, while carbon dioxide diffuses out of them, since these gases diffuse much faster through air or some other gaseous medium than through water.

In at least some aquatic plants, the circulation of gases by diffusion is augmented by mass flow driven by modestly elevated pressure. In some plants with floating or emergent leaves, active young leaves have been found to absorb air from the atmosphere, and force it down the lacunae in the petioles, using the energy of the sun's heat (Dacey, 1980). In this way, oxygen in excess of that of photosynthetic origin is supplied to the buried plant parts. A return flow, enriched with carbon dioxide, makes its way to the surface via older leaves. Even in submerged foliage, oxygen from actively photosynthesizing young foliage may flow through the stem lacunae under slightly elevated pressure.

Lacunate tissue is commonly formed by extreme dilation of the inter-cellular air spaces that normally occur in the cortical tissues and leaf mesophyll that lie outside the vascular strands; but air passages may also be formed by partial or complete dissolution and replacement of the xylem that would be present in the vascular strand of a terrestrial plant.

4. *Tolerance of Oxygen-shortage*

The tissues of roots and rhizomes buried in deep, oxygen-deficient environments possess physiological adaptations that enable them to survive periods of oxygen-deficiency. Under such conditions these tissues may respire without oxygen, forming methanol or lactic acid, rather than carbon dioxide, as waste products. This process is important during winter and at night, when darkness cuts off the supply of oxygen that in daylight originates in the leaves where photosynthesis is taking place.

5. *Reduction of Leaf Tissues*

This is common, especially in submerged leaves, which may be membranous and very thin, thread-like, or finely dissected (in Dicotyledons), providing a large surface area for gas exchange in relation to the volume of the leaf, to counteract the effect of low solubility and diffusion rate of the gases in water. Thus the internal photosynthesizing tissues (mesophyll) are in closer communication with the surrounding water. The complex mechanisms for controlling water-loss in aerial leaves are unnecessary under water. Stomata may be non-functional or absent, cuticle very reduced, and the photosynthesizing mesophyll tissue unspecialized or even absent. The epidermis may contain chlorophyll, in contrast to its usual character in land plants, and may carry out most or all of the plant's photosynthesis.

6. *Reduction of Roots*

Adaptation of aquatic life in still water may involve the reduction, even to complete elimination, of the root system, since its primary function here is for anchorage, not water absorption. Root hairs are often dispensed with. The extreme condition of this adaptation leads to the detachment of the plant from the solid bottom substratum to become freely suspended or floating, and thus independent of water depth, at least during the active growing season.

7. *Adaptive Plasticity*

Individuals of many aquatic plant species are capable of assuming widely diverse forms in response to varying environmental factors in the habitats in which they find themselves. In the structures of stems and leaves especially, they can diverge surprisingly far from the average forms for their species in response to such factors as their state of maturity, the advancing season, as reflected by the length of the daylight period, the clarity, depth or temperature of the water (Cook, 1968) or to the presence of competing vegetation. This plasticity enables a plant to exploit a complex of variable and constantly varying environments, such as the rising and falling interface between water and air, or seasonally fluctuating shores.

The plasticity of form displayed by aquatic plant species is also responsible for frequent problems in their recognition and classification. These problems must be approached with an open mind. The criteria by which differing character-expressions are used to circumscribe and distinguish these species must be accepted with a degree of flexibility that is seldom required when dealing with land plants. It is particularly important to keep in mind the possible ways in which ecological influences can affect the growth and morphology of an individual plant.

8. *Adaptation of Pollination Systems*

With increasing vegetative adaptation to life in water is found a progressive trend away from pollination systems dependent on insects to ones using the wind, or ultimately, water currents as the pollinating agents. With this trend is associated a reduction of the size of flowers to simple, inconspicuous, unisexual or even dioicous flowers. They may be floating or even perpetually submerged, some extreme developments of the latter having thread-like, entangling pollen. Many of these flowers have the capacity for self-pollination in case pollen-transfer vectors fail.

9. *Modifications of Fruit*

Since seed-eating or fruit-eating land birds and wind may be ineffective as seed dispersing agents on the water surface, aquatic plants have evolved fruits that can be dispersed by water. Some plants have fruits with spongy, buoyant tissues that allow them to float away from the parent plant. Others, especially those with many-seeded fruits, liberate the seeds through decay of the enclosing fruits under the water.

Waterfowl, by their feeding activities on or beneath the water surface, are important agents in dispersing seeds and other plant parts from one water body to another; bearing them internally or clinging to feathers or feet.

10. *Increased Reliance on Vegetative Means of Propagation*

Many aquatic plants are notably shy flowerers, and rely much more on vegetative propagation than do land plants. Some produce winter buds: special buds that are produced late in the growing season, and are shed, to lie on the bottom of a water body over winter and germinate in spring to form new plants. Other plants produce extensive over-wintering rhizomes, or tubers, containing starch or other food reserves.

Evolution and Classification of the Group

Not every adaptive modification is found in any one species or family. It would appear that, given an initial trend toward the invasion of aquatic environments by an ancestral diversifying stock, the adaptive trends have been further pursued by the diverging evolutionary branches independently of each other, to achieve parallel results. Thus we see an overall picture of a wide diversity of specializations developed independently in evolutionary lines of plants derived from a common, basically primitive stock of moisture-preferring, or amphibious, but relatively unmodified ancestors. In this respect, it is interesting to point out that most modern students of plant evolution postulate that the Monocotyledons, including this group of aquatic families, originated from an early, primitive stock of herbaceous, aquatic or amphibious Dicotyledons whose surviving dicotyledonous descendents are the modern water-lilies (*Nymphaeacea*). The relationship between the *Nymphaeaceae* and primitive Monocotyledons is indicated in many features, such as those of the stem anatomy (lack of cambium, scattered slender vascular strands, absence or near-absence of vessels), the attachment of ovules in the ovary, and of the type of pollen (Takhtajan, 1961; Cronquist, 1968).

In particular: during this process of adaptation, the flowers of many of these plants have become so profoundly modified that the resolution of their structure, and even the delimitation of the individual flower from the inflorescence of which it is part, are difficult and, for some plants, have been the subject of prolonged (for over a hundred years), and still unresolved, debate.

The varying interpretations of the structure and development of these plants, and particularly of their flowers and fruits, have given rise to a variety of conflicting hypotheses regarding the evolution of the group as a whole. Since concepts of evolution influence concepts of natural classification, these debates have led to a diversity of proposed systems of classification based on the hypothetical relationships.

A very simplified scheme of apparent evolutionary relationships among the families treated here, and some related groups, as they currently appear to the author, is presented in figure 1. Other, more comprehensive treatments of the subject are presented by Hutchinson (1959), Takhtajan (1961), Cronquist (1968), and Thorne (1976). These treatments differ among themselves in varying degrees. The scheme presented here combines features found in all of them, while retaining the families and orders in their older, and more conservative, circumscriptions except where change has appeared necessary.

It can be seen that the families are arranged in a branching pattern, not in a simple linear sequence from primitive to advanced groups. This is a reflection of the way in which various groups have independently evolved different specialized features while retaining different primitive characteristics. Thus, the sequence in which the families are dealt with in this work (see Check-list; p. 2) is only an arbitrary representation of evolutionary progress.

The vertical dimension in this scheme represents relative degree of specialization. This representation, however, is only approximate, since the diverse kinds of specialization found are often not strictly comparable between different evolutionary 'branches'.

Closeness of relationship between the families is suggested by the length of the connecting lines between them in this scheme. However, the incompleteness of our knowledge of the details of the relations and the inevitable distortion arising from the projection of a multi-dimensional 'tree' onto a two-dimensional page, make the representation of the closeness of relationship comparative rather than absolute.

THE DIAGNOSTIC KEYS

The keys are intended as an aid in the identification of plants, using the most visible characters. They are not a system of natural classification, since the family relationships among the plants are often not evident from their gross appearance.

Many aquatic plants are such shy flowerers that they are seldom found in flower or fruit. Thus it is most convenient to use readily visible features of vegetative form for determining their identity.

The classification, on the other hand, is determined on the basis of characters of flower, fruit, microscopic anatomy and development, that reflect the genetic background of the plants, but are often very difficult to observe.

Two general keys are presented on the following pages. The first is a key to all the families and genera of aquatic plants known to occur in British Columbia, including Pteridophytes and Dicotyledons. The second key deals strictly with the families and genera covered in this work. These

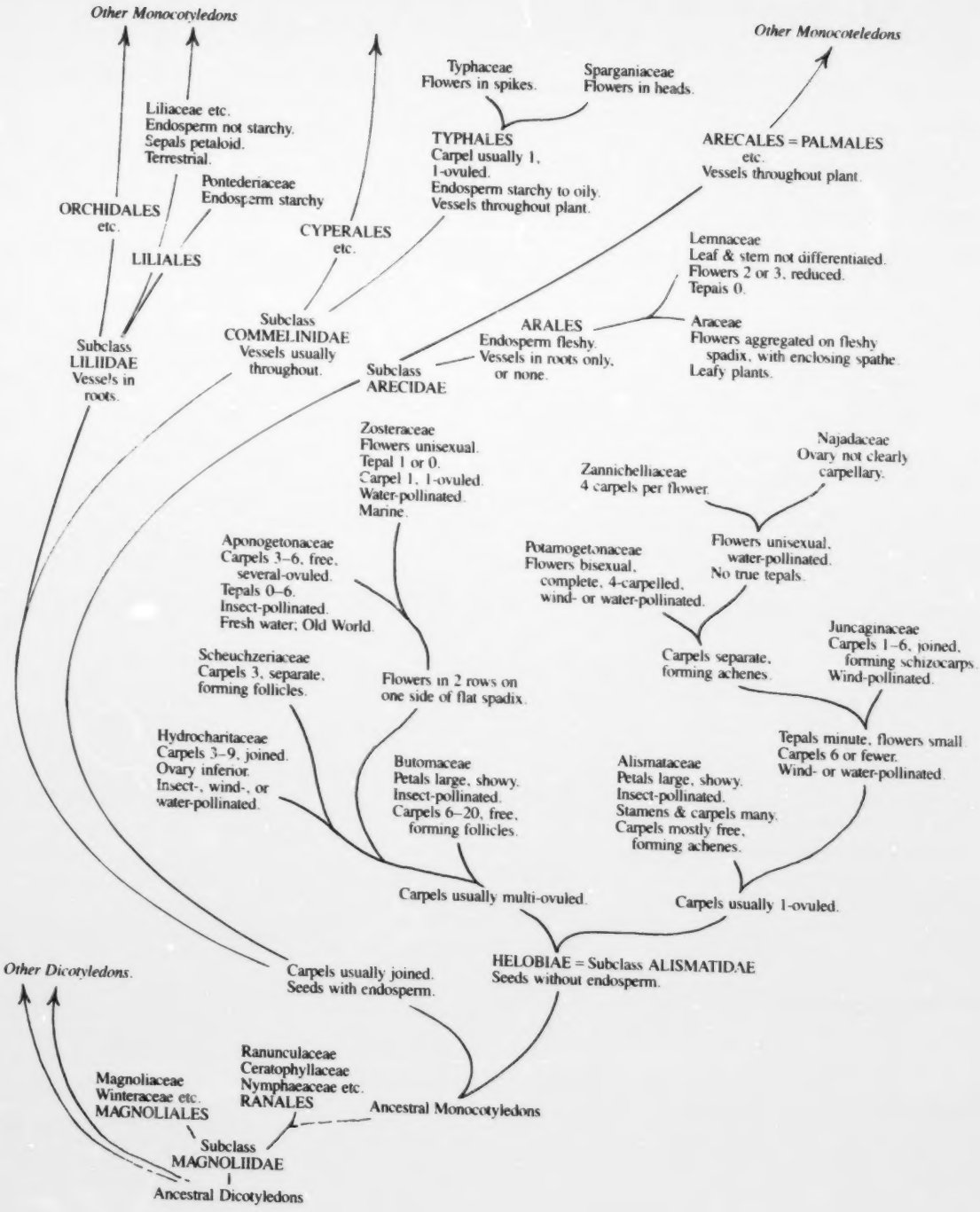


Figure 1. A simplified scheme of evolutionary relationships among the families covered in this paper, and some related groups.

keys use gross vegetative features as far as possible. They lead in many cases directly to genera rather than to families, but in these cases the generic names are followed by the names, in brackets, of the families to which they belong.

In using a key, a succession of choices is made between alternative character descriptions in numbered pairs, starting with number one. At each stage, the character-description is chosen that more nearly matches the case in hand. Each successive choice leads to the name of a genus or family or to the number of the next pair of alternatives to be chosen from. This process is repeated if necessary until the name of a plant group is reached. The description of the genus or family indicated should then be referred to for further details and keys to the species and perhaps varieties.

KEY TO FAMILIES AND GENERA OF AQUATIC PLANTS IN BRITISH COLUMBIA

1. a. Shrubs **2**
b. Herbs **11**

2. a. Bud enclosed in a single scale ..... ***Salix*** **(SALICACEAE)**
b. Bud with 2 or more scales **3**

3. a. Leaves opposite, entire **4**
b. Leaves alternate **5**

4. a. Leaves soft, deciduous. Tall shrubs, over a metre tall ..... ***Cornus stolonifera*** **(CORNACEAE)**
b. Leaves leathery, evergreen. Low shrubs, under a metre tall ..... ***Kalmia*** **(ERICACEAE)**

5. a. Leaf oblanceolate, toothed near apex, yellow-dotted, aromatic ..... ***Myrica gale*** **(MYRICACEAE)**
b. Leaf wider: lanceolate to ovate or orbicular **6**

6. a. Leaf conspicuously toothed or lobed **7**
b. Leaf entire **9**

7. a. Leaf sharply toothed or shallowly lobed. Flowers in terminal clusters, white or pink **8**
b. Leaf crenate, often shiny and leathery. Flowers in small lateral catkins ..... ***Betula*** **(BETULACEAE)**

8. a. Branchlets rather stout, with short stout lateral spurs bearing leaves and terminal clusters of white flowers. Sometimes a small tree with shredding bark ..... ***Malus diversifolia*** **(ROSACEAE)**
b. Branchlets very slender, without short lateral spurs, but with terminal dense panicles of small pink flowers ..... ***Spiraea douglasii*** **(ROSACEAE)**

9. a. Leaf scurfy with minute scales, flat, green beneath ..... ***Chamaedaphne calyculata*** **(ERICACEAE)**
b. Leaf not scurfy, with margins somewhat revolute **10**

10. a. Young twigs and undersides of leaves whitened ..... ***Andromeda polifolia*** **(ERICACEAE)**
b. Young twigs and leaves not whitened ..... ***Ledum*** **(ERICACEAE)**

11. a. Leaves absent, not differentiated, or reduced to scales, cusps, or basal sheaths **12**
b. Leaves present, with well-developed blade and/or petiole **17**

12. a. Minute free-floating plants, without distinction of stem and leaf ..... **(LEMNACEAE)**
b. Stems well developed **13**

13. a. Stem bright yellow, thread-like, twining, parasite on *Salicornia* ..... ***Cuscuta marina*** **(CUSCUTACEAE)**
b. Stem green, stout **14**

14. a. Stem conspicuously jointed at regular intervals. Leaves scale-like or almost absent **15**
b. Stem not jointed at regular intervals, with a few basal leaf sheaths only **16**

15. a. Stem succulent, solid, each joint ending in a pair of opposite low cusps. Flowers minute, in terminal succulent spikes ..... ***Salicornia*** **(CHENOPODIACEAE)**
b. Stem parchment-textured, hollow, with whorls of coherent dark scale-leaves. Spores borne in terminal cones with hexagonal sporophylls ..... ***Equisetum*** **(EQUISETACEAE)**

16. a. Spike one, clearly terminal ..... ***Eleocharis*** **(CYPERACEAE)**
b. Spikes one to many, appearing lateral near top of stem, due to stem-like upright projecting bract ..... ***Scirpus*** **(CYPERACEAE)**

17. a. Leaf compound, or deeply dissected if simple **18**
b. Leaf simple and unlobed **34**

18. a. Leaves whorled or opposite **19**
b. Leaves alternate **22**

19. a. Leaf sectors forked, of cartilaginous texture when fresh ..... ***Ceratophyllum*** **(CERATOPHYLLACEAE)**
b. Leaf pinnately or palmately dissected, not of cartilaginous texture **20**

20. a. Submersed leaves divided into at least 3 sectors at base. Emergent leaves, if any, broad and serrate ..... ***Bidens*** **(COMPOSITAE)**

b. Submersed leaves pinnately lobed or dissected **21**

21. a. Leaves mostly submersed, with filiform parts ..... ***Myriophyllum*** **(HALORAGIDACEAE)**

b. Leaves emersed, simple, flat, with lobed margins ..... ***Lycopus*** **(LABIATAE)**

22. a. Plant up to 5 cm long, normally floating, pinnately branched. Leaves minute, 2-lobed ..... ***Azolla*** **(SALVINIACEAE)**

b. Plant normally larger and rooted in mud. Leaves larger, with more than 2 lobes **23**

23. a. Leaves palmately divided or trifoliate **24**

b. Leaves pinnately or bipinnately divided **27**

24. a. Leaf with 4 fan-like leaflets ..... ***Marsilea vestita*** **(MARSILEACEAE)**

b. Leaf with odd number of leaflets, divisions or lobes **25**

25. a. Leaf with 3 elliptic, entire leaflets ..... ***Menyanthes trifoliata*** **(GENTIANACEAE)**

b. Leaf with 3 or more divisions that, if linear, are further divided or lobed **26**

26. a. Submersed or floating plant with submersed leaves divided at least twice into linear divisions. Petiole base and stipules sheathing the stem. Single white or yellow flowers ..... ***Ranunculus*** **(RANUNCULACEAE)**

b. Tall erect plant with palmately lobed, flat leaves, normally all above the water. Petiole base and stipules not forming a sheath. Pink flowers in a terminal raceme ..... ***Sidalcea hendersonii*** **(MALVACEAE)**

27. a. Plant with small bladders on leaves or stem. Leaf divisions linear or filiform ..... ***Utricularia*** **(LENTIBULARIACEAE)**

b. Plant without bladders. Leaf divisions wider, flat **28**

28. a. Leaf simply pinnate **29**

b. Leaf bipinnate, with clearly defined leaflets. Petiole base sheathing stem. Flowers small, white, in umbels **33**

29. a. Petiole base not sheathing stem **30**

b. Petiole base sheathing stem **31**

30. a. Petiole base with paired stipules. Leaflets irregular in size, sharply toothed. Erect plant ***Geum*** **(ROSACEAE)**

b. Petiole base without stipules. Leaflets ovate to nearly circular, bluntly toothed or entire. Trailing or floating plant ..... ***Rorippa nasturtium-aquaticum*** **(CRUCIFERAE)**

31. a. Leaflets clearly distinct from rachis, lanceolate, 2.5 cm or more long **32**

b. Leaf variously lobed, but without clearly differentiated leaflets and rachis. Succulent plant of sea shores with creeping rhizome, and yellow button-like rayless flower heads ..... ***Cotula coronopifolia*** **(COMPOSITAE)**

32. a. Erect plant. Leaflets more than 7 ..... ***Sium suave*** **(UMBELLIFERAE)**

b. Trailing and floating plant. Leaflets 5–7 ..... ***Potentilla palustris*** **(ROSACEAE)**

33. a. Leaf outline ½ to ⅔ as wide as long. Lateral veins of leaflets running to notches in margin, or, if leaflets entire, with bulblets in their axils. Erect plants with chambered erect rootstocks ..... ***Cicuta*** **(UMBELLIFERAE)**

b. Leaf outline broadly triangular, ⅔ to fully as wide as long. Lateral veins of leaflets running into teeth. Plant with arching stems ..... ***Oenanthe samentosa*** **(UMBELLIFERAE)**

34. a. Leaves (except bracts) in a basal tuft, or on a basal rhizome **35**

b. Leaves arising along stem (basal leaves may also be present) **64**

35. a. Leaves linear **36**

b. Leaves with expanded blades **49**

36. a. Leaf elongate, flat and ribbon-like, pliable **37**

b. Leaf stiff, ascending or spreading, or, if pliable, not flat in cross-section **40**

37. a. In fresh water **38**

b. In sea water ..... **(ZOSTERACEAE) 39**

38. a. Leaf 4–5 mm wide, entire, relatively thick and tough. No rhizome. Flowers in a panicle, perfect ..... ***Alisma gramineum*** **(ALISMATACEAE)**

b. Leaves wider and thinner, minutely toothed, from a slender rhizome. Flowers unisexual: pistillate single on a long coiling peduncle, staminate many, minute, in a basal spathe ..... ***Vallisneria*** **(HYDROCHARITACEAE)**

39. a. Rhizome short, irregular in thickness. Leaf narrow but thick and opaque. Dioicous plants with cordate fruits. On exposed, rocky coasts ... ***Phyllospadix*** **(ZOSTERACEAE)**

b. Rhizome relatively elongate, more uniform in thickness. Leaf wider or, if narrow, thin and often translucent. Monoicous plants with ellipsoid fruit. In sheltered bays and lagoons ... ***Zostera*** **(ZOSTERACEAE)**

40. a. Plant with long slender stolons giving rise to leaves or leaf tufts at intervals ... **41**

b. Plant with stout buried rhizomes or corms, or annuals ... **42**

41. a. Leaf hollow, with externally visible partitions. Flowers minute, in umbels ... ***Lilaeopsis occidentalis*** **(UMBELLIFERAE)**

b. Leaf solid, unpartitioned. Flowers single on pedicels from nodes in stolon ... ***Ranunculus flammula*** **(RANUNCULACEAE)**

42. a. Leaf triangular in cross-section. Flowers pink in a large umbel ... ***Butomus umbellatus*** **(BUTOMACEAE)**

b. Leaf not triangular in cross-section ... **43**

43. a. Leaf flattened and set edge-on to the flowering shoot, sheathing it at base. One leaf-like bract at top of peduncle. Flower spike oblique ... ***Acorus calamus*** **(ARACEAE)**

b. Leaf not set edge-on to shoot ... **44**

44. a. Leaf bases widely distended around a corm, and encolsing spore-cases packed with white spores. Usually submersed ... ***Isoetes*** **(ISOETACEAE)**

b. Leaf bases either not widely distended or not enclosing a corm ... **45**

45. a. Leaf with distinct stipular sheath, 1–10 cm long, at base. Plants of alkaline or saline marshes ... **46**

b. Leaf not sheathing at base or with a sheath not more than 5 mm long ... **47**

46. a. Annual with terete leaf, and 1-carpelled, 1-stamened flowers in a spike, with pistillate flowers in basal leaf sheaths ... ***Lilaea scilloides*** **(JUNCAGINACEAE)**

b. Perennials with short rhizomes and racemes of 3-stamened, 3-carpelled or 6-carpelled flowers. Leaf semi-circular in cross-section ... ***Triglochin*** **(JUNCAGINACEAE)**

47. a. Leaf thick, hollow, rounded at tip, spreading. Peduncle several times as long as leaves, with white flowers in a raceme above water. Plant of shallow fresh water ... ***Lobelia dortmanna*** **(LOBELIACEAE)**

b. Leaf slender, subulate, solid, ascending ... **48**

48. a. Annual with flowers in short raceme somewhat taller than the leaves. 4 sepals and 4 petals all separate. Plant of shallow fresh water ... ***Subularia aquatica*** **(CRUCIFERAE)**

b. Perennial with single flowers on scapes that are shorter than the leaves. Calyx cup-like, petals 5 joined. Plant of tidal marshes ... ***Limosella subulata*** **(SCROPHULARIACEAE)**

49. a. Leaf hollow, flask-like, with an erect 'lid', often purple ... ***Sarracenia purpurea*** **(SARRACENIACEAE)**

b. Leaf of conventional form ... **50**

50. a. Leaf margin toothed or crenate ... **51**

b. Leaf margin entire ... **54**

51. a. Underside of leaf white with fine cobwebby hair. Leaf arrowhead-shaped ... ***Petasites sagittatus*** **(COMPOSITAE)**

b. Leaf glabrous, ovate to reniform or circular. Flowers white ... **52**

52. a. Plant with short upright caudex. Upper part of stipular sheath free from petiole, as a ligule ... ***Caltha*** **(RANUNCULACEAE)**

b. Plant with creeping rhizome or stolons ... **53**

53. a. Rhizome stout. Stipular sheath entirely joined to petiole, thus no ligule. Flowers in a raceme ... ***Fauria crista-galli*** **(GENTIANACEAE)**

b. Rhizome or stolon thread-like. Flower solitary ... ***Viola palustris*** **(VIOLACEAE)**

54. a. Leaf blade with deep basal sinus ... **55**

b. Leaf blade tapering to truncate or subcordate at base ... **59**

55. b. Leaf apex acuminate or acute ... **56**

b. Leaf apex rounded. Leaf often large, floating ... **57**

56. a. Leaf blade arrowhead-shaped. Flowers in whorls, white ... ***Sagittaria*** **(ALISMATACEAE)**

b. Leaf blade heart-shaped. Flowers in a dense spike (spadix) surrounded by a white spathe ... ***Calla palustris*** **(ARACEAE)**

57. a. Coarse plant, often with floating leaves 10–30 cm across, from a massive horizontal submerged rhizome. Flowers large, yellow ... **58**

b. Smaller plant, up to 35 cm tall, inhabiting swamps. Leaves 1–4 cm across. Flower small, white ... ***Parnassia*** **(SAXIFRAGACEAE)**

58. **a.** Leaf margin rounded on either side of a deep basal sinus. Flower yellow ... ***Nuphar*** **(NYMPHAEACEAE)**
b. Leaf margin cuspidate on either side of the basal sinus. Flower white or pink ... ***Nymphaea*** **(NYMPHAEACEAE)**

59. **a.** Leaf blade 40–150 cm long, conspicuously netted-veined. Flowers in a dense spadix surrounded by a yellow spathe ... ***Lysichiton americanum*** **(ARACEAE)**
b. Leaf blade much smaller, usually 1–10 cm long ... **60**

60. **a.** Plant not stoloniferous ... **61**
b. Plant stoloniferous. Flowers solitary on scapes ... **63**

61. **a.** Flowers in panicles with whorled branches ... ***Alisma*** **(ALISMATACEAE)**
b. Flower solitary at top of stem ... **62**

62. **a.** Leaf palmately veined. Stem often with conspicuous sessile bract near middle. Flower white ... ***Parnassia*** **(SAXIFRAGACEAE)**
b. Leaf pinnately veined. Flower blue to purple, spurred ... ***Pinguicula*** **(LENTIBULARIACEAE)**

63. **a.** Leaf blade much shorter than petiole, rounded at apex. Plant densely tufted. Calyx cup-like, the sepals joined ... ***Limosella aquatica*** **(SCROPHULARIACEAE)**
b. Leaf blade shorter than to longer than petiole, or absent, acute at apex. Plant stoloniferous. Sepals separate ... ***Ranunculus flammula*** **(RANUNCULACEAE)**

64. **a.** Leaves alternate ... **65**
b. Leaves opposite, subopposite, or whorled ... **93**

65. **a.** Leaves linear or narrowly lanceolate, often no distinction between blade and petiole ... **66**
b. At least some leaves with wide blades, either sessile or with distinct petioles ... **86**

66. **a.** Leaves set edge-on to stem ... **67**
b. Leaves flat side to stem, or cylindrical ... **69**

67. **a.** Leaves 1 cm or more wide. Plant up to a metre or more tall. Flowers large, yellow ... ***Iris pseudacorus*** **(IRIDACEAE)**
b. Leaves less than 1 cm wide. Plant seldom over 30 cm tall ... **68**

68. **a.** Flowers minute, crowded in dense brown heads ... ***Juncus ensifolius*** **(JUNCACEAE)**
b. Flowers few, on pedicels, yellow ... ***Sisyrinchium californicum*** **(IRIDACEAE)**

69. **a.** Stem triangular in cross-section, solid. Leaves 3-ranked. Flowers minute, in scaly spikes ... **70**
b. Stem not triangular in cross-section ... **71**

70. **a.** Flowers of 2 kinds, staminate and pistillate, without perianth bristles ... ***Carex*** **(CYPERACEAE)**
b. Flowers all bisexual, with perianth bristles ... ***Scirpus*** **(CYPERACEAE)**

71. **a.** Leaf base not expanded into a sheath around the stem. Glabrous, succulent plants of alkaline or saline marshes. Flowers minute, coloured as the foliage ... ***Suaeda*** **(CHENOPODIACEAE)**
b. Leaf base or petiole sheathing the stem ... **72**

72. **a.** Stem hollow. Flowers 2-ranked in small scaly spikes ... **73**
b. Stem solid ... **74**

73. **a.** Nodes noticeably swollen and solid. Internodes straight. Leaves 2-ranked, with very long sheaths and blades diverging from the top. Flowers in spikelets in a terminal panicle ... **(GRAMINEAE)**
b. Nodes not swollen. Leaves clearly 3-ranked. Flower spikes in axillary racemes ... ***Dulichium arundinaceum*** **(CYPERACEAE)**

74. **a.** Plant erect ... **75**
b. Plant with slender, flaccid, submerged stems ... **80**

75. **a.** Flowers in dense globular heads, green to whitish ... ***Sparganium*** **(SPARGANIACEAE)**
b. Flowers in spikes, panicles, or asymmetric heads ... **76**

76. **a.** Flowers in conspicuous terminal spikes; the staminate spike above the pistillate one. Tall stout-stemmed plant with erect, pale green leaves ... ***Typha latifolia*** **(TYPHACEAE)**
b. Flowers all alike, perfect, in small spikes or other arrangements. Smaller plants with slender stems ... **77**

77. **a.** Leaves with apical pores. Flowers in racemes. Fruits 3 follicles per flower ... ***Scheuchzeria palustris*** **(SCHEUCHZERIACEAE)**
b. Leaves without apical pores. Flowers not in racemes ... **78**

78. **a.** Stem terminating in one or more small scaly flower spike. Fruits achenes with conspicuous long hairs, collectively forming a conspicuous cottony tuft ... ***Eriophorum*** **(CYPERACEAE)**
b. Stem bearing clusters of small scaly flowers or flower spikes. Fruits without conspicuous cottony hairs ... **79**

79. a. Flowers 2 or 3 in each of many tiny whitish spikes in 1–3 clusters. Perianth of 10–12 very short bristles. Plants of peat bogs ... ***Rhynchospora alba*** **(CYPERACEAE)**

b. Flowers with 6 tepals of chaffy texture; brown or green, never white ... ***Juncus*** **(JUNCACEAE)**

80. a. Ligule absent or, if formed, less than 1 mm long ... **81**

b. Ligule distinct, 2 mm or more long, or the stipular sheath free from the leaf or petiole base, and thus all ligule ... **84**

81. a. Leaves filiform. Flowers with 6 chaffy textured tepals. Fruit a capsule ... ***Juncus*** **(JUNCACEAE)**

b. Leaves ribbon-like, elongate ... **82**

82. a. Plants of fresh water. Flowers in globular heads ... ***Sparganium*** **(SPARGANIACEAE)**

b. Plants of the sea or tidal lagoons. Flowers in flat spikes enclosed in sheathing leaf bases ... **83**

83. a. Dioicous plants with cordate fruit. Rhizomes short, irregular in thickness. Leaf narrow but thick and opaque. On exposed, rocky coasts ... ***Phyllospadix*** **(ZOSTERACEAE)**

b. Monoicous plants with ellipsoidal fruit. Rhizomes more uniform in thickness, relatively elongate. Leaf wider or, if narrow, thin and often translucent. In sheltered bays and lagoons ... ***Zostera*** **(ZOSTERACEAE)**

84. a. Leaves narrowly lanceolate, tapering to base and apex, opaque, all alike, parallel-veined. Submerged. Flowers pale yellow, with 6 tepals and long hypanthium, emerging from stipular sheaths ... ***Heteranthera dubia*** **(PONTEDERIACEAE)**

b. Leaves linear and parallel-veined or, if tapering, the submersed leaves translucent, with evident cross-veins between the parallel longitudinal veins. Flowers in a terminal spike; green, minute, with 2 or more tepals and no hypanthium ... **(POTAMOGETONACEAE) 85**

85. a. Flowers 2 per spike, with 2 stamens and 2 tepals. Achenes stipitate, 4. Leaves filiform. Peduncle often long and coiled ... ***Ruppia maritima*** **(POTAMOGETONACEAE)**

b. Flowers more than 2 per spike, with 4 tepals and 4 stamens. Achenes sessile. Peduncle stouter, never coiled. Leaves diverse ... ***Potamogeton*** **(POTAMOGETONACEAE)**

86. a. Leaf peltate, purple beneath. Submerged parts of plant covered with mucilage when young. Flowers solitary, dull purple ... ***Brasenia schreberi*** **(NYMPHAEACEAE)**

b. Leaf marginally attached, not peltate ... **87**

87. a. Stipular sheath absent. Plant with short stiff appressed hairs. Flowers blue, small, in one-sided, uncoiling racemes ... ***Myosotis*** **(BORAGINACEAE)**

b. Stipular sheath present ... **88**

88. a. Stipular sheath free from leaf or petiole base, or, if attached, leaves of two kinds: floating leaves wider and thicker than submersed ones ... ***Potamogeton*** **(POTAMOGETONACEAE)**

b. Stipular sheath attached to leaf base or petiole base, at least on basal leaves. Leaves all alike ... **89**

89. a. Leaf netted-veined ... **90**

b. Leaf parallel-veined from base or with closely parallel lateral veins from a midvein, entire ... **91**

90. a. Leaf broadly elliptic, circular to reniform, palmately veined, crenate or toothed. Flowers single or few, not spicate ... ***Caltha*** **(RANUNCULACEAE)**

b. Leaf lanceolate to elliptic ovate, pinnately veined, entire. Flowers in a terminal spike, commonly pink ... ***Polygonum*** **(POLYGONACEAE)**

91. a. Leaf lanceolate, tapering to base and apex. Flowers 1 or 2, pale yellow, emerging from stipular sheath ... ***Heteranthera dubia*** **(PONTEDERIACEAE)**

b. Leaf ovate or broadly heart-shaped, cordate-based ... **92**

92. a. Leaf apex acuminate to attenuate. Flowers minute, white, in a spadix 2–4 cm long, subtended by a white spathe ... ***Calla palustris*** **(ARACEAE)**

b. Leaf apex rounded or blunt. Flowers blue, in a spike 6–15 cm long, subtended by a small green bract ... ***Pontederia cordata*** **(PONTEDERIACEAE)**

93. a. Leaves in whorls of 3 to many ... **94**

b. Leaves opposite ... **96**

94. a. Leaves in whorls of 4 to many, narrow, entire. Plant submersed or the top often emergent ... ***Hippuris vulgaris*** **(HIPPURIDACEAE)**

b. Leaves in whorls of 3 to 6, finely serrulate ... **95**

95. a. Tall stout upright plants with broadly lanceolate, netted-veined leaves. Flowers conspicuous, pink, spurred, very sweet-scented. Not always aquatic ... ***Impatiens glandulifera*** **(BALSAMINACEAE)**

b. Submerged, slender plant with small, 1-veined, translucent leaves. Flowers white, floating, seldom seen ... ***Elodea*** **(HYDROCHARITACEAE)**

96. a. Leaves, though appearing opposite, really subopposite, the base and sheath of one of each pair arising within the sheath of the other ... **97**

b. Leaves truly opposite ... **98**

97. **a.** Leaf serrulate, continuous with its sheath ... ***Najas flexilis*** **(NAJADACEAE)**
b. Leaf entire. Sheath separate ... ***Zannichellia palustris*** **(ZANNICHELLIACEAE)**

98. **a.** Leaf margin toothed ... **99**
b. Leaf margin entire ... **107**

99. **a.** Flowers in terminal heads with yellow ray-flowers. Leaves pinnately many-veined, serrate and sometimes deeply dissected ... ***Bidens*** **(COMPOSITAE)**
b. Flowers not in terminal heads with yellow ray-flowers ... **100**

100. **a.** Flowers 1–3 per leaf axil ... **101**
b. Flowers several in each axillary cluster ... **103**

101. **a.** Flowers small, pale yellow to white. Calyx of 5 sepals. Corolla 5-lobed at mouth ... ***Gratiola*** **SCROPHULARIACEAE)**
b. Flowers relatively large and showy. Calyx and corolla 2-lipped ... **102**

102. **a.** Flowers blue. Calyx with helmet-like crest on top ... ***Scutellaria galericulata*** **(LABIATAE)**
b. Flowers yellow or red. Calyx without a crest on top ... ***Mimulus*** **(SCROPHULARIACEAE)**

103. **a.** Flowers in racemes, usually blue ... **104**
b. Flowers in dense axillary clusters, which may be congested together upward to form a thick spike. Stem 4-sided ... **(LABIATAE) 105**

104. **a.** Corolla wide open, 4-lobed. Calyx without a dorsal crest. Fruit a 2-lobed capsule ... ***Veronica*** **(SCROPHULARIACEAE)**
b. Corolla tubular, 2-lipped at mouth. Calyx with dorsal crest. Fruit 4 nutlets per flower ... ***Scutellaria lateriflora*** **(LABIATAE)**

105. **a.** Flower clusters absent from uppermost leaf axils. Plant soft-hairy, with mint-like scent when crushed ... ***Mentha arvensis*** **(LABIATAE)**
b. Flower clusters in middle and upper axils ... **106**

106. **a.** Foliage almost glabrous; the hairs visible only under magnification. Flowers minute, white. Plant scentless ... ***Lycopus*** **(LABIATAE)**
b. Foliage distinctly rough-hairy. Flowers larger, mauve to pink or blue. Plant rank-smelling when crushed ... ***Stachys*** **(LABIATAE)**

107. **a.** Plant with white stipules between the paired linear leaves ... ***Spergularia*** **(CARYOPHYLLACEAE)**
b. Stipules absent ... **108**

108. **a.** Inflorescence or flowers terminal ... **109**
b. Inflorescence or flowers axillary ... **115**

109. **a.** Plants generally stiffly erect, not at all fleshy ... **110**
b. Plants sprawling, often rooting at nodes, with ascending branch ends or, if plant erect, fleshy ... **113**

110. **a.** Plant less than 30 cm tall, the stems usually several in a clump. Leaves elliptic, 2–6 cm long ... **111**
b. Plant 30 cm to 2 m tall. Leaves lanceolate 4–8 cm long. Flowers in terminal racemes, opening wide ... **112**

111. **a.** Flowers yellow, opening wide. Leaves and petals with black or clear dots ... ***Hypericum*** **(HYPERICACEAE)**
b. Flowers blue, generally closed ... ***Gentiana sceptrum*** **(GENTIANACEAE)**

112. **a.** Plant usually 30–100 cm tall. Leaves lanceolate, tapering to bases, black-dotted. Flowers yellow ... ***Lysimachia terrestris*** **(PRIMULACEAE)**
b. Plant a metre or more tall. Leaves broadly rounded to cordate at base. Flowers pink to purple ... ***Lythrum salicaria*** **(LYTHRACEAE)**

113. **a.** Small plant with leaves 0.5–2 cm long ... **114**
b. Larger, fleshy plant with leaves 2–4 cm long, leaf bases joined around the stem. Flowers in a terminal head ... ***Jaumea carnosa*** **(COMPOSITAE)**

114. **a.** Flowers single, flesh-coloured to yellowish. Sepals 5. Leaves and petals with minute black or clear dots ... ***Hypericum*** **(HYPERICACEAE)**
b. Flowers in terminal racemes, whitish. Sepals 2. Leaves undotted ... ***Montia fontana*** **(PORTULACACEAE)**

115. **a.** Flowers in racemes ... **116**
b. Flowers not in racemes ... **117**

116. **a.** Leaves with dark dots. Stem upright. Flowers yellow, in racemes from lower leaf axils ... ***Lysimachia thyrsiflora*** **(PRIMULACEAE)**
b. Leaves not dotted. Stems trailing with ascending branches. Flowers white, pink, or blue ... ***Veronica*** **(SCROPHULARIACEAE)**

117. **a.** Leaves sessile, at least if submerged, or no differentiation between petiole and blade ... **118**
b. Leaves with petioles ... **123**

118. a. Leaf bases sheathing stem. Flowers minute, axillary sessile to short-stalked. Minute plant with linear fleshy leaves ***Tillaea aquatica*** **(CRASSULACEAE)**
b. Leaf bases not sheathing stem **119**

119. a. Flowers on pedicels 1 cm or more long ***Gratiola*** **(SCROPHULARIACEAE)**
b. Flowers sessile or subsessile **120**

120. a. Leaves cordate-based. Erect emergent plant. Flowers minute, in a small cluster in each axil. Capsule globose ***Ammannia coccinea*** **(LYTHRACEAE)**
b. Leaves not or scarcely cordate-based **121**

121. a. Leaves membranous, at least the submerged ones linear-lanceolate with truncate or notched apices. Floating or terrestrial leaves, if present, petioled, spatulate, 3-veined. Stems filiform, trailing. Flowers minute, green, usually one in an axil ***Callitriche*** **(CALLITRICHACEAE)**
b. Leaves fleshy, elliptic. Stem relatively stout, trailing or erect **122**

122. a. Leaves dotted (most visible in young leaves). Flowers in the lower axils. Calyx cup-like, pink. Petals none. In saline or alkaline marshes ***Glaux maritima*** **(PRIMULACEAE)**
b. Leaves not dotted. Flowers in upper axils or terminal. Calyx of free sepals, green. Petals small, whitish. On sea beaches ***Honkenya peploides*** **(CARYOPHYLLACEAE)**

123. a. Leaf blade ovate. Petiole fringed with white hairs. Flowers yellow, conspicuous, on axillary pedicels ***Lysimachia ciliata*** **(PRIMULACEAE)**
b. Leaf blade elliptic to spatulate. Flowers sessile **124**

124. a. Erect emergent plant. Fruit a globose capsule ***Rotala ramosior*** **(LYTHRACEAE)**
b. Trailing, floating or matted plant **125**

125. a. Leaf blade acute at apex ***Ludwigia palustris*** **(ONAGRACEAE)**
b. Leaf blade rounded to notched at apex **126**

126. a. Leaf blade 3-veined from base. Apex rounded or notched. Stipules none. Flower without petals. Fruit a disc-like schizocarp splitting into 4 1-seeded parts ***Callitriche*** **(CALLITRICHACEAE)**
b. Leaf blade pinnately veined. Apex shallowly notched. Stipules present, minute. Flower with 3 minute petals. Fruit a globose capsule ***Elatine*** **(ELATINACEAE)**

KEY TO FAMILIES AND GENERA COVERED BY THIS BOOK

1. a. Minute free-floating plants without distinction of stems or leaves **LEMNACEAE**
b. Plants with differentiated stems and leaves **2**

2. a. Leaves all basal **3**
b. Plants with leafy stems; often also with basal leaves **13**

3. a. Mid-tidal or subtidal marine plants with flat, ribbon-like leaves **ZOSTERACEAE**
b. Plants of fresh to brackish waters or marshes, or, if in the sea, leaves not flat or ribbon-like **4**

4. a. Leaves with broad, expanded blades **5**
b. Leaves linear **7**

5. a. Leaves heart-shaped, closely parallel-veined ***Calla*** **(ARACEAE)**
b. Leaves not heart-shaped, with conspicuous cross-veins, forming a net with the main veins **6**

6. a. Leaves pinnately netted-veined, very large, elliptic to broadly lanceolate ***Lysichiton*** **(ARACEAE)**
b. Leaves with open parallel venation and numerous oblique cross-veins **ALISMATACEAE**

7. a. Leaves flat, ribbon-like **8**
b. Leaves thick, triangular, circular, or semi-circular in cross-section **10**

8. a. Leaves arranged edge-on to stem ***Acorus*** **(ARACEAE)**
b. Leaves placed conventionally: Face to stem **9**

9. a. Leaves ribbon-like, with acute to rounded tips and scattered marginal teeth. Pistillate with single flowers on long coiling peduncles. Staminate with basal ensheathed clusters. ***Vallisneria*** **(HYDROCHARITACEAE)**
b. Leaves gradually tapering to acute or acuminate tips or, if ribbon-like, without marginal teeth. Flowers in whorls or panicles **ALISMATACEAE**

10. a. Leaf triangular in cross-section, erect. Flowers in a false umbel, pink, showy ***Butomus*** **(BUTOMACEAE)**
b. Leaf terete or semi-terete in cross-section. Flowers in racemes or spikes **11**

11. a. Leaves terete. Flowers in spikes ***Lilaea*** **(JUNCAGINACEAE)**
b. Leaves semi-terete. Flowers in racemes **12**

12. a. Leaves with apical pores. Racemes with bracts and up to 5 flowers ... *Scheuchzeria* (SCHEUCHZERIACEAE)
    b. Leaves without apical pores. Racemes bractless, with 8 to many flowers ... *Triglochin* (JUNCAGINACEAE)

13. a. Leaf with upstanding, emergent, heart-shaped blade, with closely parallel lateral veins ... 14
    b. Leaf linear, or if with an expanded blade, the blade floating or submersed ... 15

14. a. Visible stem erect, bearing 1 or 2 leaves and a spike of blue flowers ... *Pontederia* (PONTEDERIACEAE)
    b. Visible stem trailing, bearing ascending leaves and white spathe and spadix ... *Calla* (ARACEAE)

15. a. Flowers in dense globular heads. Leaves linear ... *Sparganium* (SPARGANIACEAE)
    b. Flowers not in heads. Leaves various ... 16

16. a. Leaves erect, strap-like. Flowers in conspicuous spikes ... *Typha* (TYPHACEAE)
    b. Leaves floating or submersed ... 17

17. a. Leaves subopposite or whorled ... 18
    b. Leaves mainly alternate ... 20

18. a. Leaves in whorls usually of 3. The whorls often crowded ... *Elodea* (HYDROCHARITACEAE)
    b. Leaves subopposite, with minute flowers or fruit at their bases ... 19

19. a. Leaves oblong-lanceolate, serrulate, their bases not surrounded by a sheath ... *Najas* (NAJADACEAE)
    b. Leaves linear, entire, the bases of a pair surrounded by a funnel-like sheath when young ... *Zannichellia* (ZANNICHELLIACEAE)

20. a. Plants of marine or intertidal habitats, with elongate, ribbon-like leaves ... ZOSTERACEAE
    b. Plants of fresh-water habitats or, if marine or intertidal, leaves not ribbon-like ... 21

21. a. Leaves slenderly lanceolate, tapered to bases and apices, adherent at bases to stipular sheaths. Flowers 1 or 2 in axils, complete, pale yellow, with long hypanthium ... *Heteranthera* (PONTEDERIACEAE)
    b. At least the submersed leaves either filiform, with untapered bases adherent to sheaths, or free from sheaths and linear and flat, lanceolate, or broader. Flowers in terminal spikes, minute, greenish, without hypanthium ... POTAMOGETONACEAE

DESCRIPTIONS OF FAMILIES, GENERA AND SPECIES

The Family BUTOMACEAE

Perennial aquatic herbs of diverse habit, often with milky juice. Flowers solitary or in false umbels that are really very condensed cymose panicles based on a fundamentally alternate branching habit in which pairs of successive internodes fail to elongate. The inflorescence is cymose, the terminal flower of each branch forming first, followed by others formed in succession from buds formed in the axils of prophylls at the bases of the branches (Singh and Sattler, 1974).

Flowers with three usually small sepals, three relatively large showy petals, 8 to many stamens, 6–20 carpels in a whorl, free from each other or almost so, and with or without styles. Ovules numerous, scattered over the inner surface of the carpel. The ventral margins of the carpel never join, as they do in most flowering plants, but are merely pressed together.

Fruits are whorls of follicles containing many seeds, that are liberated by the separation of the ventral carpel margins. Seeds have straight or horseshoe-shaped embryos and no endosperm.

A family of five genera, mostly tropical, in both the Old and New Worlds. One temperate genus is represented here.

The Genus *BUTOMUS* L.

Rhizomatous herb with linear basal leaves two-ranked on the rhizome and triangular in cross-section above.

Inflorescence an umbel-like cyme terminating a scape, with a false whorl of three bracts, commonly with two buds in the axil of each bract, and as many axillary branch systems producing terminal flowers followed by later flowers derived from successively developed buds in the axils of basal prophylls. Thus the flowers open in succession and the false 'umbel' is repeatedly replenished by the development of younger flowers through at least the early summer (Charlton and Ahmed, 1973).

Flowers with both the sepals and petals coloured showy pink to purplish, and persistent into the fruiting stage. Stamens 9, carpels usually 6, tapering into styles, intially distinct, but becoming

coherent at their bases by fruiting stage through upgrowth of a ring of underlying tissue. The numerous ovules scattered over the lateral inside walls of the carpels. Stigmas on the upper inner margins of the styles. In each flower, the pollen is shed before the stigmas are receptive.

At fruiting stage the mature follicles open by separation of the formerly appressed ventral carpel margins. Seeds longitudinally ribbed, with straight embryos and no endosperm.

***Butomus umbellatus* L.** **Flowering-rush**

The only species: Characteristics of the genus.

Native to temperate Eurasia, this species has been introduced into North America. It is grown as an ornamental plant for aquatic or marshy sites because of its attractive, showy flowers. It is now widespread on this continent, but has so far been collected in British Columbia only at Hatzic Lake, where it forms small colonies near the shore in water 40 to 70 cm deep (*see* map p. 130).

The Family HYDROCHARITACEAE

Frog-bit Family

Mostly dioicous herbs of fresh waters, with diverse vegetative form. Flowers one or more arising in a sessile, or pedunculate, axillary spathe consisting of one or more fused bracts. Sepals and petals three each, or the petals lacking; the bases of the perianth parts often united into a hypanthium which may be tubular and elongated. Staminate flower with 2 to 12 stamens. Pistillate flower with an inferior 3-carpelled (in ours) but unilocular ovary, and bilobed stigmas. The ovary matures into an indehiscent many-seeded fruit.

KEY TO GENERA IN BRITISH COLUMBIA

1. a. Stem rooted in bottom sediment, with long, ribbon-like basal leaves ..... ***Vallisneria***
   b. Stem with regularly spaced whorls or pairs of small ovate or lanceolate leaves. Plant sometimes becoming freely suspended in the water ..... ***Elodea***

The Genus *ELODEA* Michaux (*ANACHARIS* Richard)

Water Weed

Rooting or suspended dioicous perennials with whorled or opposite leaves regularly distributed along slender branching stems. Leaves small, ovate to lanceolate, veinless except for the midvein, the blade mostly two cells thick, consisting of the epidermal layers. Axillary scales occur in pairs. Scattered long shiny roots arise from occasional nodes along the stem.

Staminate flower usually one per spathe, sessile but sometimes apparently stalked through elongation of the floral base (hypanthium), and consisting of 3 sepals, 3 petals, and 3 to 9 stamens. Pistillate flower solitary, the greatly elongated hypanthium raising the sepals, petals and stigmas (3 of each) to the water surface.

KEY TO SPECIES

1. a. Leaves in whorls of 3 to 6, 2 cm or more long ..... ***E. densa***
   b. Leaves in whorls of 3, or occasionally opposite, shorter *2*

2. a. Leaves ovate or broadly lanceolate, entire or with a few teeth near apex. Staminate flower apparently stalked by elongation of the floral base (hypanthium) ..... ***E. canadensis***
   b. Leaves narrowly lanceolate and tapering from near the base, serrulate on margins. Staminate flower sessile, and detached for pollination ..... ***E. nuttallii***

***Elodea canadensis* Richard in Michaux** **Canada Water Weed**

***Anacharis canadensis* (Richard) Planchon**

Stems bearing opposite leaves at first, but later, and mainly, leaves in whorls of three, often crowded and recurving. Leaves ovate to broadly lanceolate, obtuse or rounded at apex, entire or with a few minute apical teeth, 6–15 mm long by 1–4 mm wide. Mesophyll tissue is practically absent from the leaf, and photosynthesis is carried out by the epidermis.

Flowers white. Staminate flower arising from a spathe, with an elongate tubular hypanthium raising the flower to the water surface. Sepals elliptic, about 4–5 mm long; petals lanceolate, as long

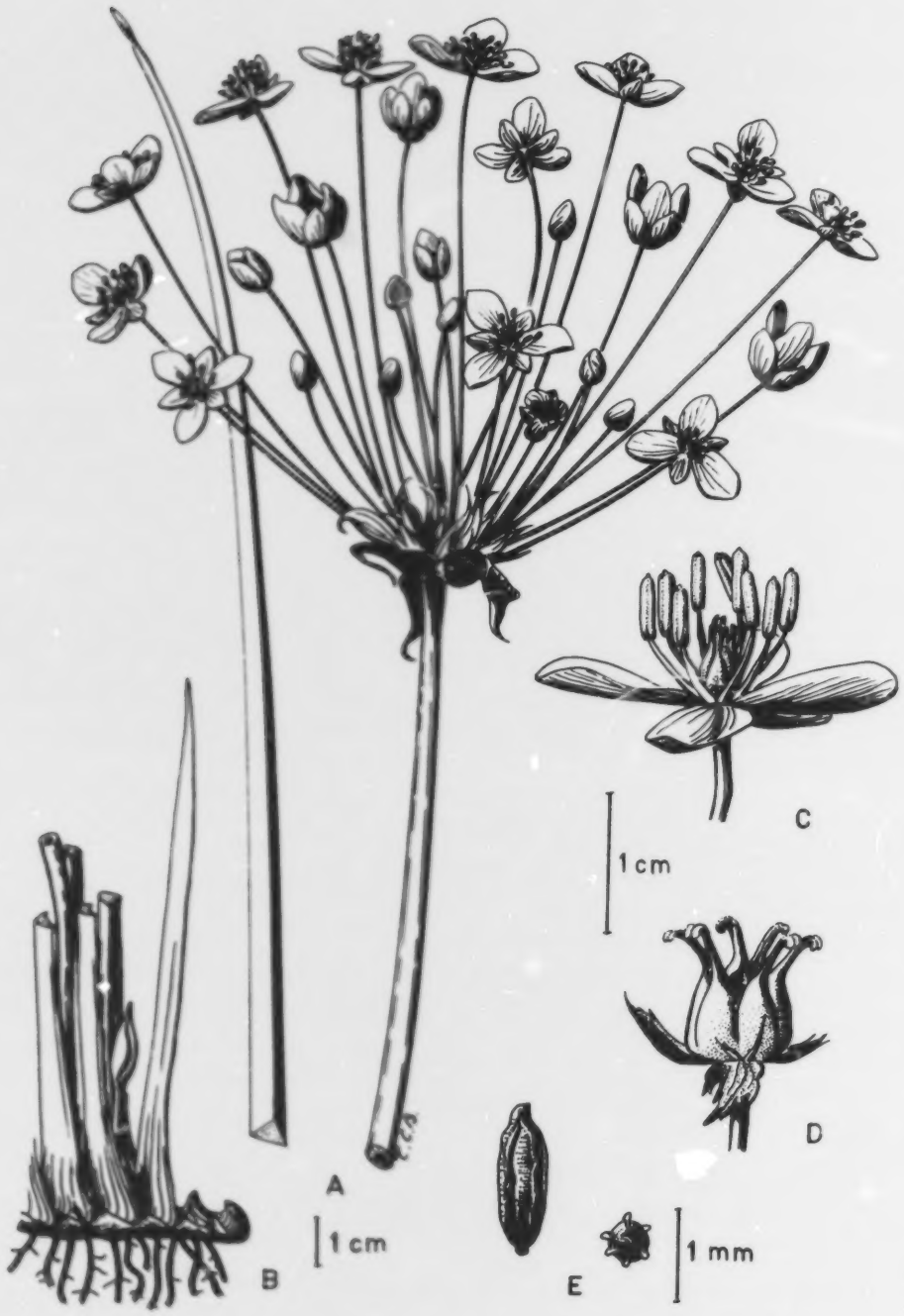


Figure 2. *Butomus umbellatus*: A, inflorescence and leaf apex; B, rhizome and shoot base; C, flower; D, fruit (cluster of follicles); E, seeds.

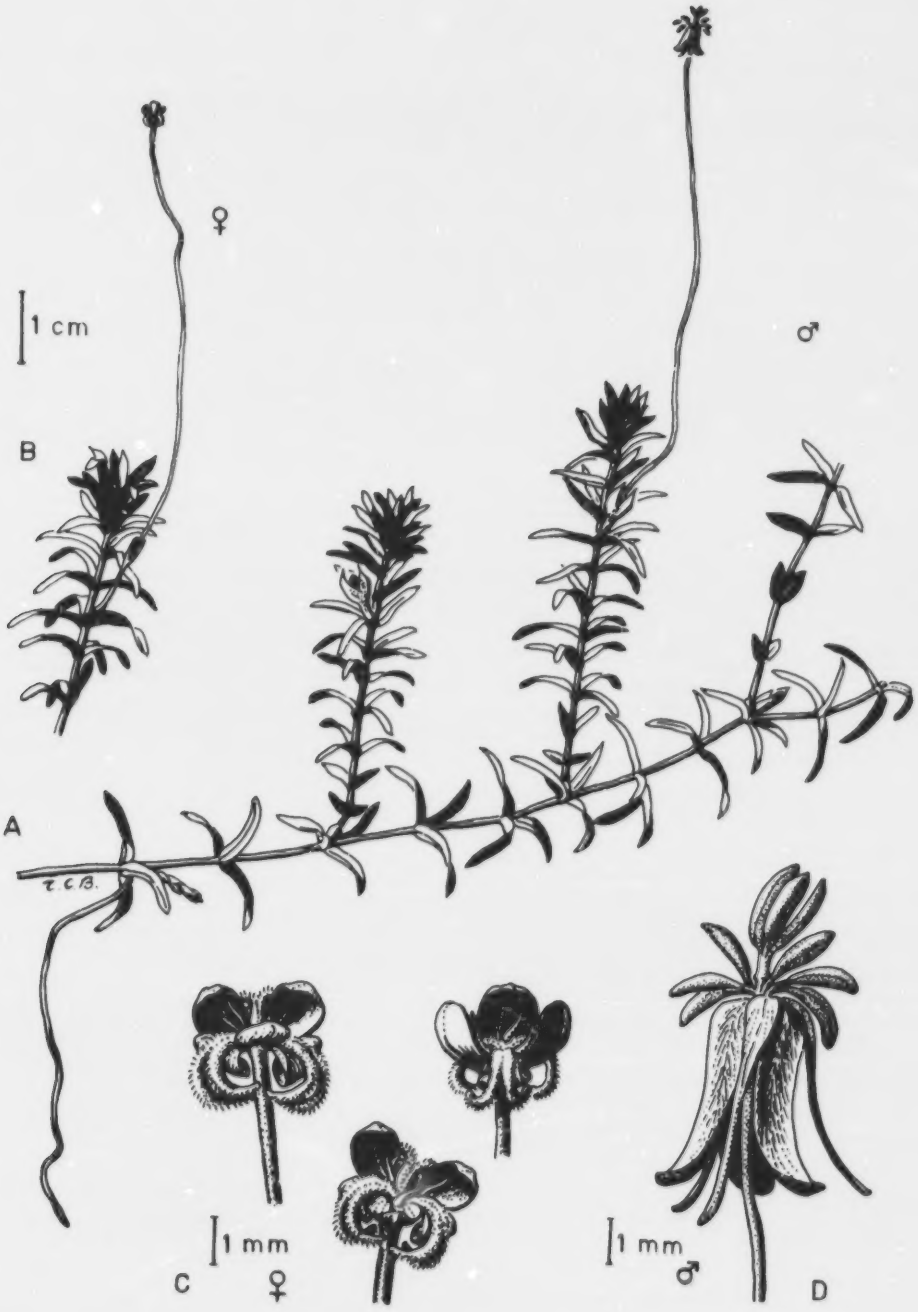


Figure 3. *Elodea canadensis*: A, staminate flowering shoot and flower; B, pistillate flowering shoot; C, pistillate flowers (upper part); D, staminate flower.

or longer; stamens 9, the inner 3 or more on a common staminal column or tube. The non-wetting pollen grains are liberated by explosive rupture of the anthers, and float across the water surface to the stigmas of the pistillate flowers.

Pistillate flower arising from a sessile 2-toothed spathe; with a thread-like hypanthium that may be up to 30 cm long, raising the flower to the water surface; subequal sepals and petals 2–2.5 mm long, 3 horn-like staminodes 0.5–1.5 mm long, and three 2-lobed white stigmas whose tips are recurved between the sepals and petals to make contact with the water-borne pollen. Capsule 6 mm long, seeds 4 mm long.

A widespread North American aquatic weed, now also well established in the Old World. It becomes particularly abundant in some polluted lakes, where it forms extensive floating and suspended mats. The plant can occur in shallow water or in water up to 3 m deep. Commonly attached to the bottom early in the season, it later often becomes detached from the bottom, and suspended at or just beneath the water surface. Flowering between July and September; large areas often flowering at once. Flowers are seldom collected, however, being sporadic in occurrence, and easily overlooked when present because of their small size. Vegetative perennation occurs through the production of turions: shoot apices with short internodes enclosed in densely overlapping foliage (*see* map p. 130).

***Elodea densa* (Planchon) Caspary**
***Egeria densa* Planchon**

A relatively coarse, sparsely branched species, rooted to the bottom or suspended in the water; at least the upper parts of the plant densely leafy, the closely spaced nodes of the stem bearing whorls of 4 to 6 leaves with overlapping bases on the upper stem, and whorls of 3 leaves near the base.

Leaves 2–3.5 cm long by about 2 mm wide or more, lanceolate, tapering from near the bases to acuminate tips, with sharply serrulate margins.

Flowers relatively large and showy for *Elodea;* both pistillate and staminate flowers permanently attached to the plant, sessile, arising from axillary spathes. Hypanthium thread-like, elongate to 6 cm. The staminate flowers 2 to several, appearing successively from an apically notched spathe that is open to the base on one side. Sepals 3–5 mm long, ovate, greenish; petals 7–9 mm long, broadly elliptic or obovate to suborbicular, white; stamens 9, separate.

Native to South America, this species has been extensively introduced in other lands, and has become a pest in some warmer countries. It is cultivated in aquaria and garden ponds, from which it may be 'liberated' into nearby natural waters, where it can maintain itself and spread by vegetative means, such as by fragmentation. Only staminate plants are known in North America, reflecting the nature of the originally introduced plant. This species has been reported from Florence and Langford Lakes, near Victoria (*see* map p. 131).

***Elodea nuttallii* (Planchon) St. John** **Nuttall's Water Weed**
***Anacharis nuttallii* Planchon**

Similar in form to *E. canadensis*, but tending more to remain rooted in bottom sediments. Leaves apparently less crowded, in whorls of 3 or occasionally 4; or opposite at the lowest nodes of a shoot; narrowly lanceolate, 6 to 13 (rarely to 20) mm long by 1.5 mm or less (rarely to 2 mm) wide; tapering from near the base to an acute apex, the margin serrulate. Leaves on flowering stems noticeably smaller and more abruptly tapering than those on sterile shoots.

Staminate spathe sessile, globose, 2–3 mm wide, with two projecting tips, containing one flower. Staminate flower initially sessile within its spathe, but at pollen maturity breaking free from the spathe, which opens at least half way to the base on one side to release it. The flower, still as a closed bud, floats to the water surface; there to open, and be drifted by wind to a pistillate flower, the anthers open, and the non-wetting pollen may be shed onto the water surface. Sepals about 2 mm long, white or marked with purplish; petals smaller or absent; stamens 9.

Pistillate spathe sessile, tubular, with an oblique orifice and notched tip. Pistillate flower sessile in its spathe, with a slender hypanthium up to 10 cm long. Sepals and petals about 1.5 mm long; 3 staminodes about 0.5 mm long; stigmas 3, shallowly bilobed or notched at apex, purplish; ovary in the base of the spathe, with 5 or 6 ovules. Capsule 5–7 mm long, seeds 4 mm long.

Widespread in central and eastern North America, with a few outliers in the British Isles. In British Columbia mainly in the southern Kootenay region, where it is uncommon in shallow water with clay or silty bottom, in lakes or backwaters of rivers. Flowers are produced in September, but are very seldom collected (*see* map p. 131).

Figure 4. *Elodea densa*: A, flowering shoot (staminate); B, staminate flower.

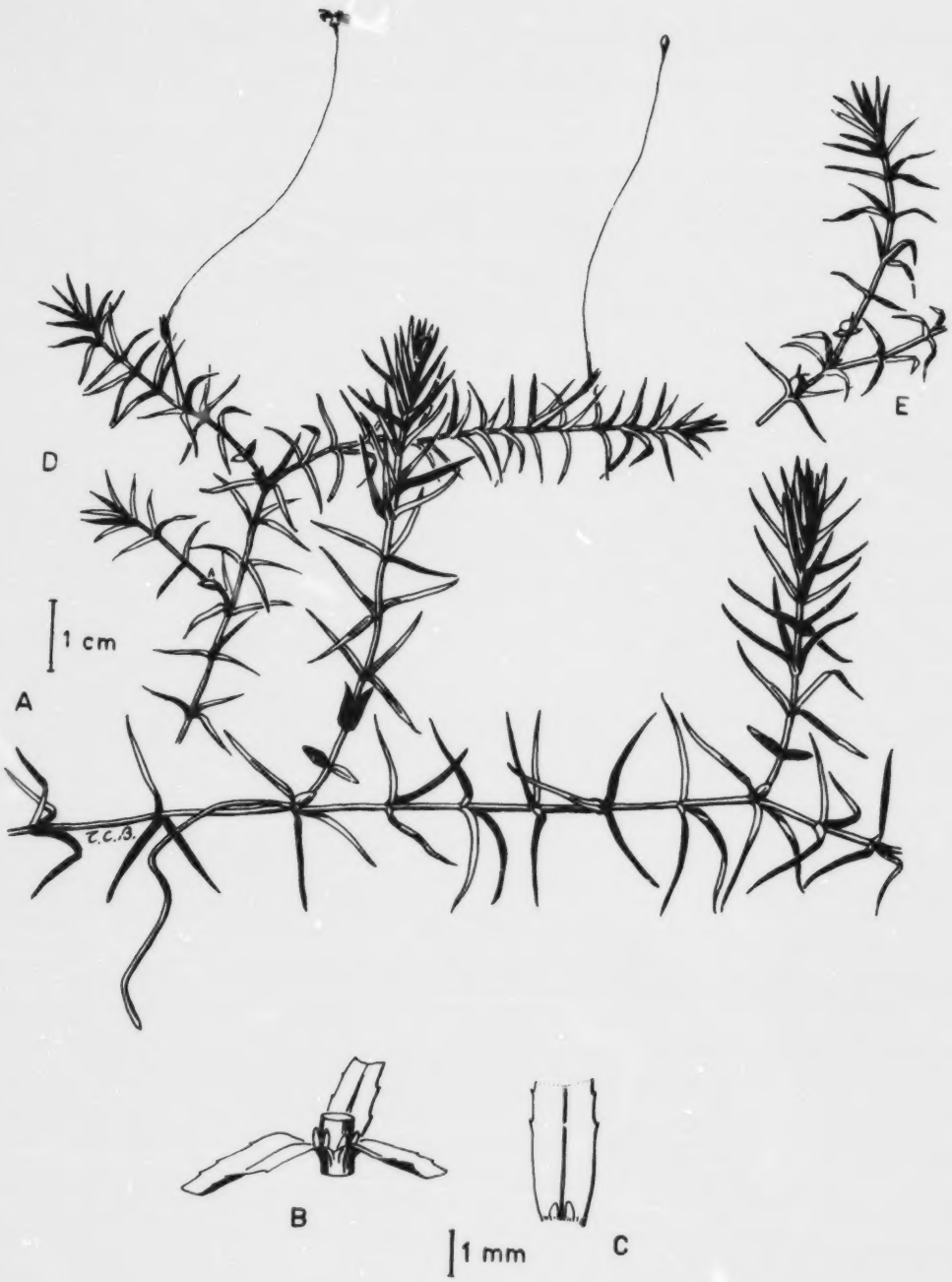


Figure 5. *Elodea nuttallii* (habit): A, sterile shoot; B, node of stem, leaf bases and axillary scales; C, leaf base showing axillary scales; D, pistillate flowering shoot; E, staminate flowering shoot.

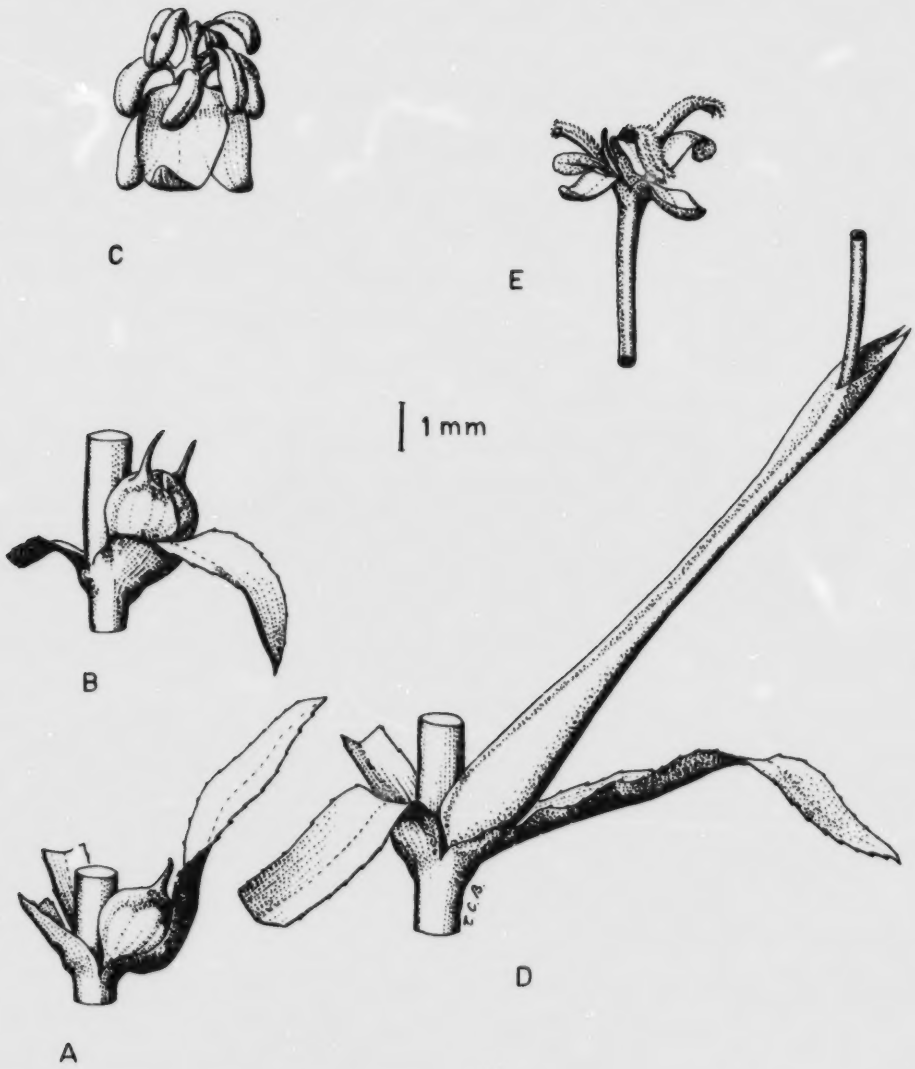


Figure 6. *Elodea nuttallii* (spathes and flowers): A, staminate spathe (closed); B, staminate spathe (open) with enclosed flower bud; C, staminate flower; D, pistillate spathe with emerging flower base (hypanthium); E, pistillate flower (upper part).

The Genus *VALLISNERIA* L.

Tapegrass

Submerged rhizomatous perennial with shoots arising at intervals from the slender rhizome. Leaves tufted, basal, ribbon-like, their length depending on water depth.

Plants dioicous; flowers arising within a spathe on the end of a peduncle which is short in staminate, and greatly elongate in pistillate plants. Staminate flowers minute, densely aggregated in a spathe, and consisting of 3 sepals, 1–3 petals, and 2 stamens. Pistillate flower solitary in a 2-lobed sheathing spathe, and consisting of an elongate inferior ovary crowned by the 3 sepals, 3 petals, and 3 forked, spreading, shortly villous stigmas.

For pollination, the staminate flowerbuds break free of the plant with the rupture of the spathe, and float up to the water surface, where they burst open, then drift with the wind to pistillate flowers, which float with the calyx, corolla and stigmas exposed.

***Vallisneria americana* Michaux** **American Tapegrass**

Leaves tapered toward the tips to rounded or acute apices, usually minutely toothed, especially near the tips; often reddish in colour; their length varying up to 2 m long according to the depth of water, the tips floating or submerged; the width from 5 to 20 mm; with 3 or more parallel longitudinal veins and scattered cross-veins.

Staminate spathe 1–2 cm long, tapered at base into a short stout peduncle up to 5 cm long by 1.5–3 mm thick, or nearly sessile; each spathe containing hundreds of crowded, minute, white flowerbuds on short pedicels. The staminate flower, when open, about 1 mm long, with 3 unequal sepals about 0.5–0.8 mm long, one minute petal, an obliquely upstanding fertile stamen with its filament partially divided into nearly parallel branches bearing exposed pollen masses of relatively few grains, and a minute staminode. Pistillate peduncle greatly elongated and helically coiled, or merely curved, shiny, and often the most conspicuous part of the plant as seen from above. Pistillate spathe 2–3 cm long, 2-lobed at apex, loosely surrounding the ovary of the solitary flower. Pistillate flower whitish, with 3 sepals 5–6 mm long, 3 minute petals, 3 minute staminodes, and 3 conspicuous, forked stigmas. The flower floats, often nearly horizontally, with the sepals resting on the water.

At pollination, the floating staminate flowers and the pistillate flower, once in contact, are held together by the depressed meniscus of the water surface; waves or other water movement tip the staminate flower onto the stigmas, enabling the transfer of pollen (Svedelius, 1932). The fruit, elongating to 5–7 cm, is drawn beneath the water for ripening by the coiling or curving of the peduncle, but for a while it may lie horizontally at the surface. The many tiny seeds are ultimately liberated by decay of the fruit.

It is not certain whether this species is native or introduced in British Columbia. Found commonly in eastern North America, it has been found in Christina Lake and in a few lakes on southern Vancouver Island. It is found in still water, commonly around a metre in depth.

In other parts of its range, this species is regarded as an important food source for waterfowl (Fassett, 1940). The buds terminating the rhizomes are eaten by diving ducks, and other parts are eaten by non-divers (*see* map p. 132).

The Family SCHEUCHZERIACEAE

Scheuchzeria Family

Rush-like bog plants with short rhizomes bearing persistent leaf-bases and leafy lower stems.

Leaves with prominently ligulate sheathing bases, semi-cylindrical blades and apical pores.

Inflorescence a terminal, bracted, few-flowered raceme of trimerous flowers. Each flower arises in the axil of a bract, bears six tepals, six stamens, and three (rarely more) separate carpels, each containing one to three ovules.

The fruits are widely spreading, short-beaked, inflated follicles, each containing one to three seeds.

One genus of one species: *Scheuchzeria palustris*, widespread in the colder parts of the Northern Hemisphere, in acid *Sphagnum* bogs.

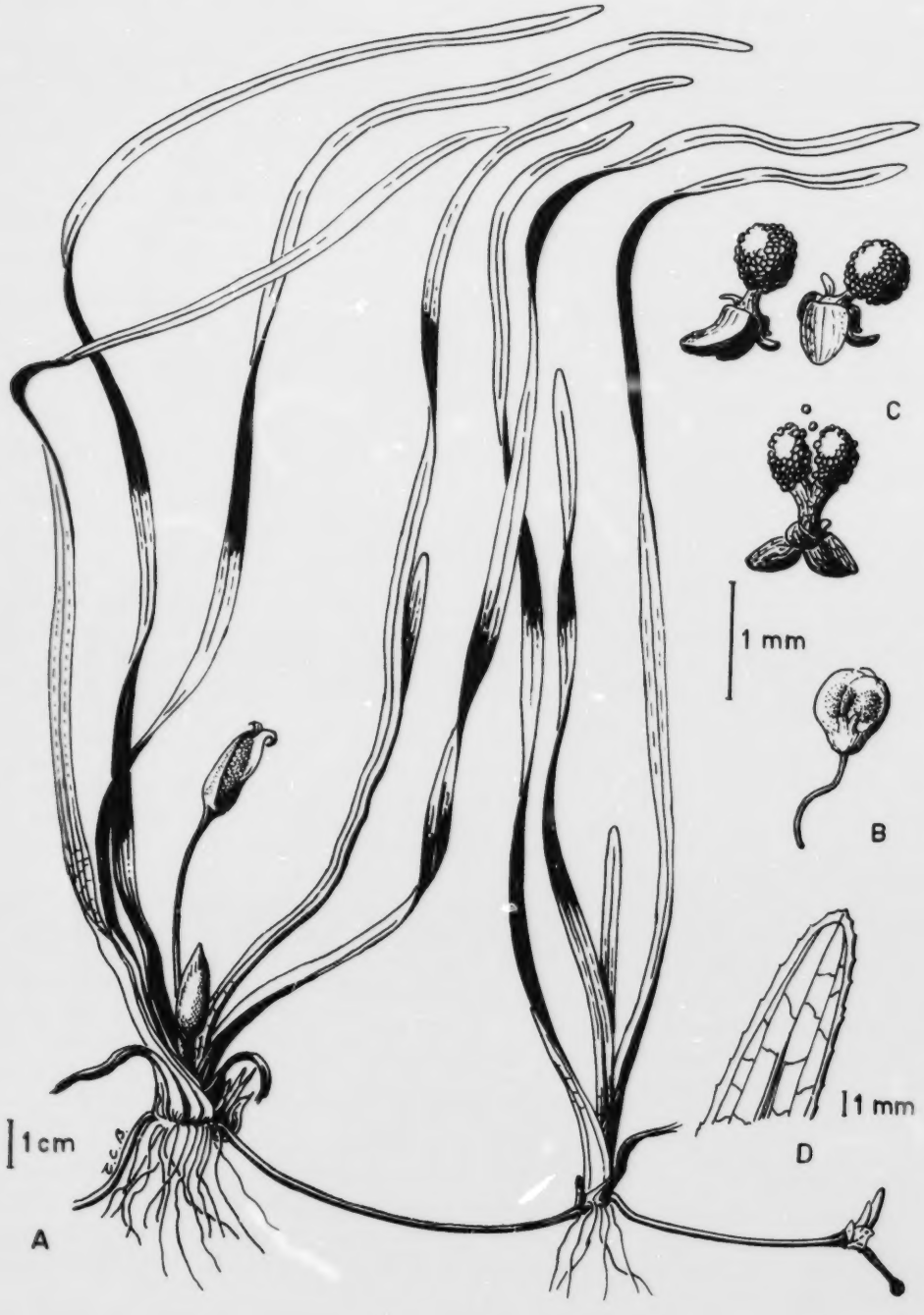


Figure 7. *Vallisneria americana* (staminate plant): A, shallow-water plant in flower with closed and open spathes containing flower masses; B, staminate flower (unopened); C, staminate flowers (open); D, leaf apex.

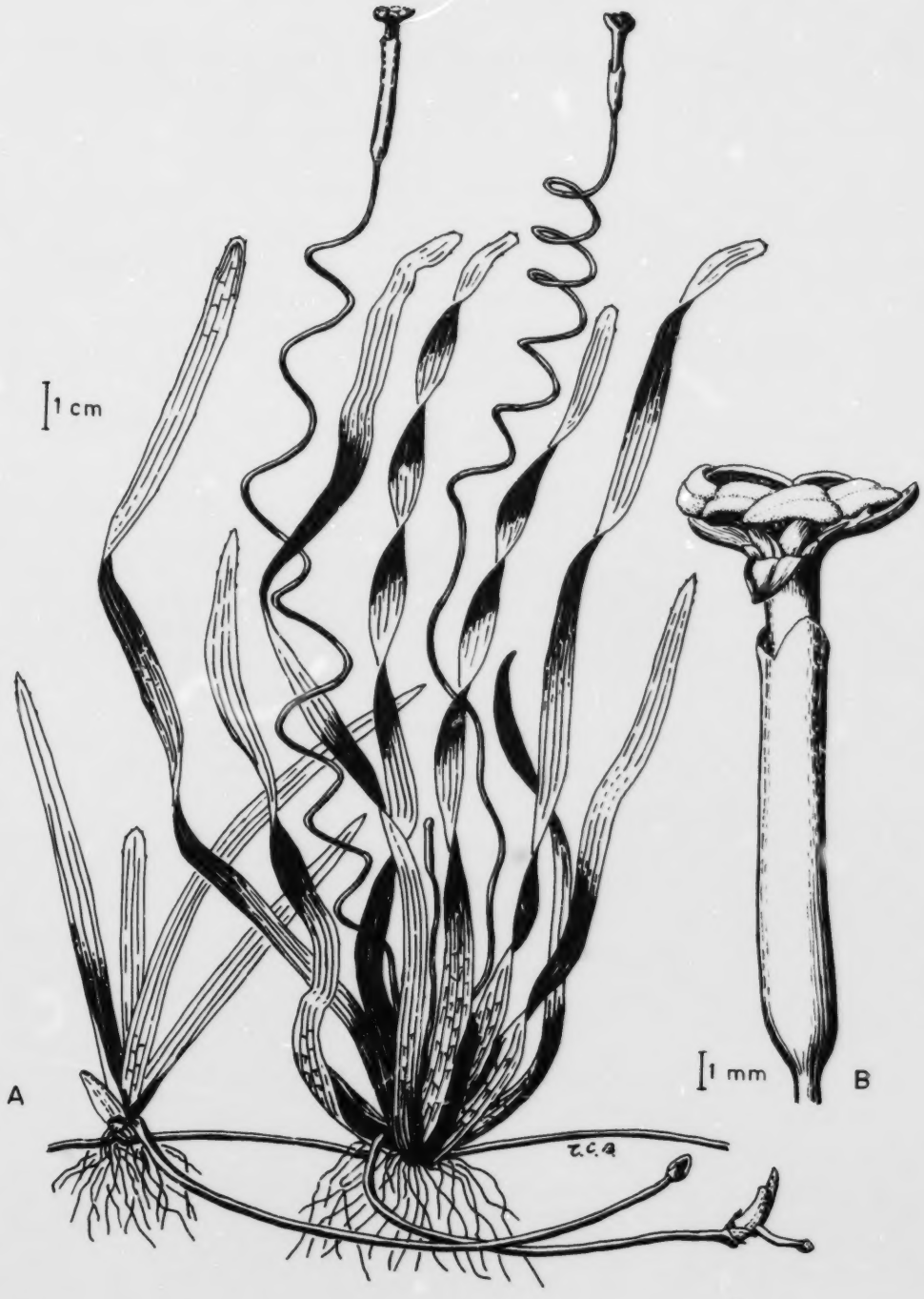


Figure 8. *Vallisneria americana* (pistillate plant): A, shallow-water plant in flower; B, pistillate flower.

***Scheuchzeria palustris* L. var. *americana* Fernald**

Growing 1–4 dm high, with pale greenish-white flowers 5–6 mm across, with lanceolate, acute or obtuse tepals, and follicles 5–10 mm long with a beak up to 1 mm long, and seeds up to 5 mm long.

The Old World var. *palustris* differs in rather smaller flowers, fruits and seeds (*see* map p. 132).

The Family ZOSTERACEAE

Sea-grass Family

Marine perennials with creeping rhizomes rooting at the nodes and giving rise to fertile shoots with elongate stems, stemless or short-stemmed sterile shoots, and long, flexible, ribbon-like, two-ranked leaves with parallel longitudinal veins, scattered cross-veins, and intervening air channels (lacunae). The tensile strength of the leaf is enhanced by the presence, beneath the epidermis, of numbers of fine longitudinal strands of sclerenchyma. Axillary scales often present.

The inflorescence is a flat spadix enveloped in the sheathing base of a leaf-like bract (spathe). The spadix bears sessile, unisexual flowers (according to one interpretation) in two rows on one face, and often bears a row of infra-marginal appendages beside the flowers. These appendages may be termed 'bractlets', 'tepals' or 'retinacula' by authors, according to interpretation. The exact homology of the structures of the inflorescence and flowers in Zosteraceae are a matter of debate (Den Hartog, 1970). Corresponding appendages in the related Old World family Aponogetonaceae are tepals, and this term is used here. The staminate flower comprises a single anther, with or without a lateral tepal. The anther comprises two sessile anther-sacs connected by a low ridge, each anther-sac containing two pollen masses. The pollen grains are thread-like and adhesive. The pistillate flower is a unilocular ovary of one carpel, with a style and two linear stigmas, and contains one ovule. A lateral tepal is present in most species. Pollination is mediated by water currents beneath the sea surface. The pollen threads, liberated in clouds, can entangle with and adhere to the bristle-like stigmas. The fruit is an achene, or a utricle that is eventually ruptured to free the single seed.

There are five genera: our two, primarily temperate genera, and three more in the tropics.

KEY TO GENERA

1. **a.** Rhizome short, irregular in thickness. Leaves narrow but thick and opaque. Dioicous, fruit cordate. Generally on exposed coasts ..... ***Phyllospadix***
   b. Rhizome relatively elongate, more uniform in thickness. Leaves wide or, if narrow, thin and often translucent. Monoicous. Fruit ellipsoid with an apical horn. Generally in sheltered bays and lagoons, on silty, gravelly or sandy substratum ..... ***Zostera***

The Genus *PHYLLOSPADIX* Hooker

Surf-grass

Dioicous perennials with irregularly knotty rhizomes fitting the roughnesses of the rock to which they are attached, and bearing stout flattish roots densely clothed with matted root-hairs. Stems flattish. Sterile shoots with short stems enclosed in leaf sheaths. Fertile shoots with longer, exposed stems.

Leaves two-ranked, ribbon-like, usually 3–5 veined, with the intervening air passages occupying half or less of the thickness of the leaf. Leaf sheaths with open, firm, pale margins that end above in rounded auricles. Leaf tips rounded, if present, but commonly becoming eroded away by surf action. Leaf blade rather thick and opaque, very dark when dry. The foliage is evergreen where not exposed for long periods at low tide.

Inflorescence a flat spadix enclosed in the distended sheath of a leaf-like bract, the blade of which tends to disintegrate before the true leaves. The spadix bears a row of infra-marginal tepals along each edge, one tepal for each flower. In the staminate inflorescence these tepals are opposite the anthers; at pollination time they spread apart and reflex, holding the margins of the spathe apart, exposing the anthers and allowing the pollen free access to the open water. In the pistillate inflorescence the tepals alternate with the ovaries and spread apart slightly when the fruit is formed and the fruiting spadix protrudes from the spathe in a convex arc. The spadix has an apical, flat, sterile extension that projects from the upper part of the enveloping sheath.

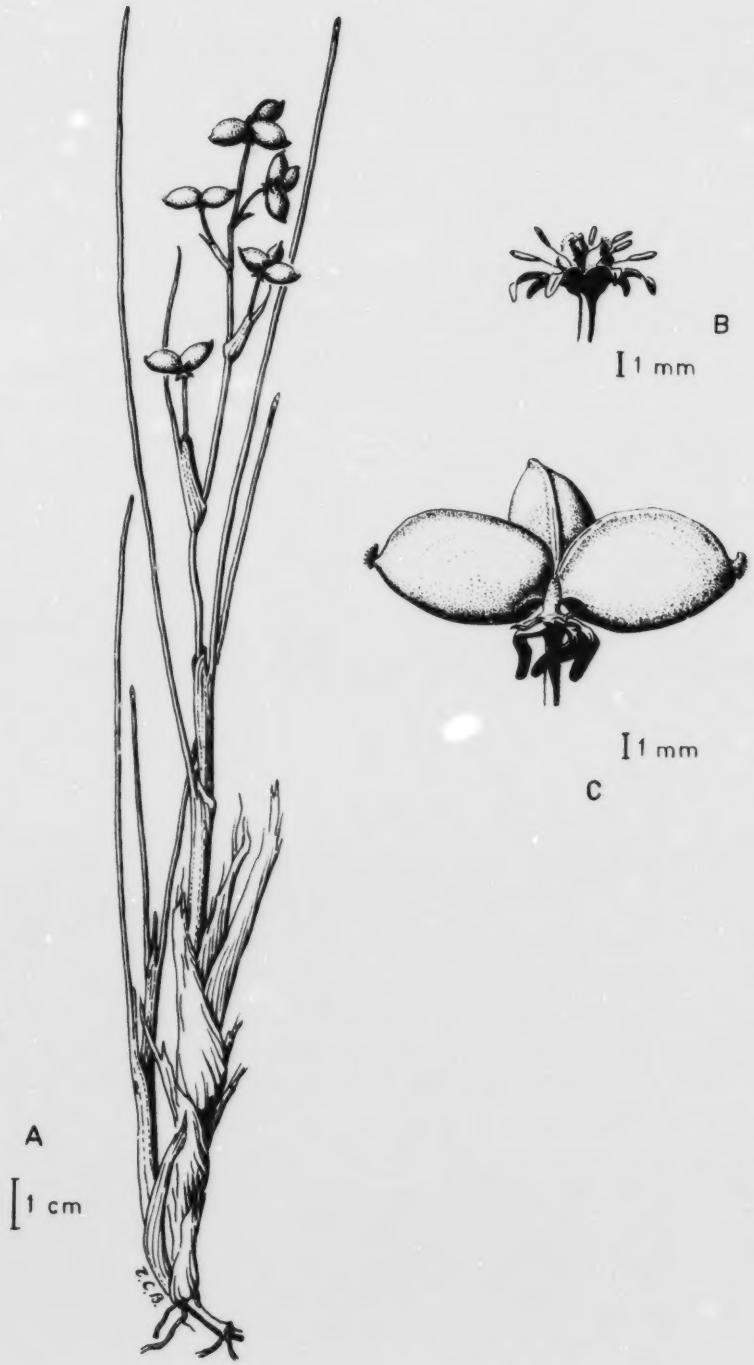


Figure 9. *Scheuchzeria palustris*: A, fruiting plant; B, flower; C, fruit (3 follicles).

The staminate flower has a single anther with two separate anther-sacs. The pistillate flower has a naked, sessile ovary with a style and two linear stigmas, containing one ovule. The fruit is a cordate- or sagittate-based achene, beaked by the style unless this has been eroded away, and containing one seed.

The genus *Phyllospadix* consists of five species distributed along the shores of the northern Pacific Ocean: our three, and two more in eastern Asia.

KEY TO SPECIES

1. **a.** Stem of fertile shoot 4–12 dm long, with branches, and spathes often paired at the nodes — ***P. torreyi***
   b. Stem of fertile shoot short 0.5–4 dm long, unbranched, normally bearing a single spathe — **2**

2. **a.** Leaf with 3, rarely 5, longitudinal veins, and entire margins — ***P. scouleri***
   b. Leaf with 5, or sometimes 7, longitudinal veins, and margins toothed toward the apex — ***P. serrulatus***

Phyllospadix typically inhabits exposed rocky shores, where it is subject to the heaviest surf. Its masses of long, ribbon-like, intensely green foliage are often seen fringing rock pools at or near the low tide level. The surf erodes and shreds the ends of the leaves so that they are seldom found intact except when young. However, these leaves are able to renew themselves by growth at their bases. The bases of the plants are nearly always submerged, in rock pools or below low tide level.

Where they occur together, our three species tend to occupy different levels or zones. *Phyllospadix serrulatus* occurs highest in the intertidal zone, with *P. scouleri* somewhat lower, while *P. torreyi* extends deep into subtidal levels. The ranges however overlap and, in places, the species may be found growing together. Where not in competition with each other, any one of the species may invade the subtidal zone (Phillips, 1979).

In our species, pistillate plants outnumber staminate ones by at least ten to one. This extraordinary sex-ratio may be a reflection on the efficiency of the pollination mechanism and seed production as a means of dispersal, or, on the other hand, may point to the evolution of a system in which pollination is unnecessary for embryo and seed development.

The achene, after shedding, loses its outer layer (exocarp) by decay, leaving a series of stiff, bark-like cells projecting from the inner side of each basal arm. This grappling arrangement serves to anchor the achene to any fibrous substratum for germination; and may also aid in dispersal by swimming birds or mammals. On the other hand, it appears most unlikely that plant fragments, once torn loose from the rocks to which they had been attached, could become reattached elsewhere in their boisterous environment. They are generally cast up on nearby beaches to contribute to the strand lines of desiccating seaweed and driftwood.

Phyllospadix scouleri Hooker

Plant with irregularly knotty rhizome fitting the roughness of the rock, to which it is attached by short, stout, flattish roots densely matted with root-hairs. Fertile stem up to 4 dm long, but usually much shorter (5–15 cm), unbranched, with 1–4 internodes and short-lived bract-leaves at the nodes, and bearing a single spathe.

Leaves up to 1.5 m long and 1½–4 mm wide, entire or rarely microscopically toothed, with 3, or occasionally 5, veins, rounded at the apex when young. Lacunae in a single layer.

Staminate inflorescences 5–6 cm long. Pistillate inflorescences 4–5 cm long, with (9-) 12–24 flowers. Mature fruit 3–4 mm long, cordate-based. Stem of pistillate inflorescence short at flowering time, and elongating somewhat as the fruit matures.

Distributed from southeastern Alaska to Baja California and Mexico, this is generally the commonest of our species of *Phyllospadix*. It is often a conspicuous member of the mid-intertidal to subtidal plant communities on exposed rocky shores on the west coast of Vancouver Island and at a few localities on the Strait of Georgia (*see* map p. 133).

Phyllospadix serrulatus Ruprecht ex Ascherson

Rhizome knotty and irregular, with short internodes, as in *P. scouleri*. Fertile stems usually very short (1–6 cm) with one internode and no nodal leaves.

Leaves, on the average, shorter, wider (2–5½ mm), and thinner than those of *P. scouleri;* with 5, or sometimes 7, longitudinal veins, and margins toothed toward the apices with minute colourless teeth (sometimes abraded away). Young leaves with broadly rounded to truncate apices. Lacunae in one layer, very slender.

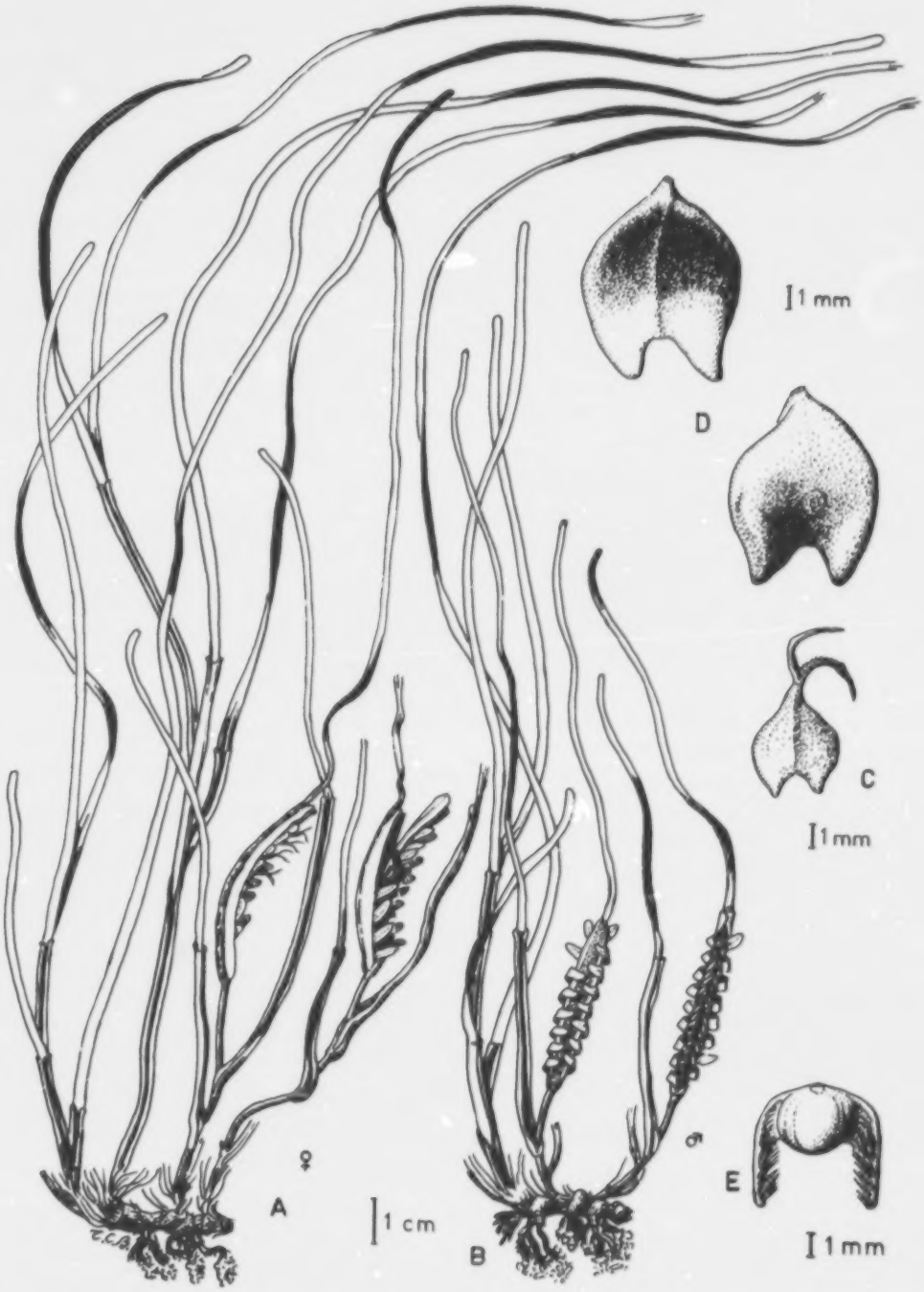


Figure 10. *Phyllospadix scouleri*: A, pistillate plant in flower; B, staminate plant in flower; C, pistillate flower; D, achenes; E, partly decayed achene showing barb-like bristles.

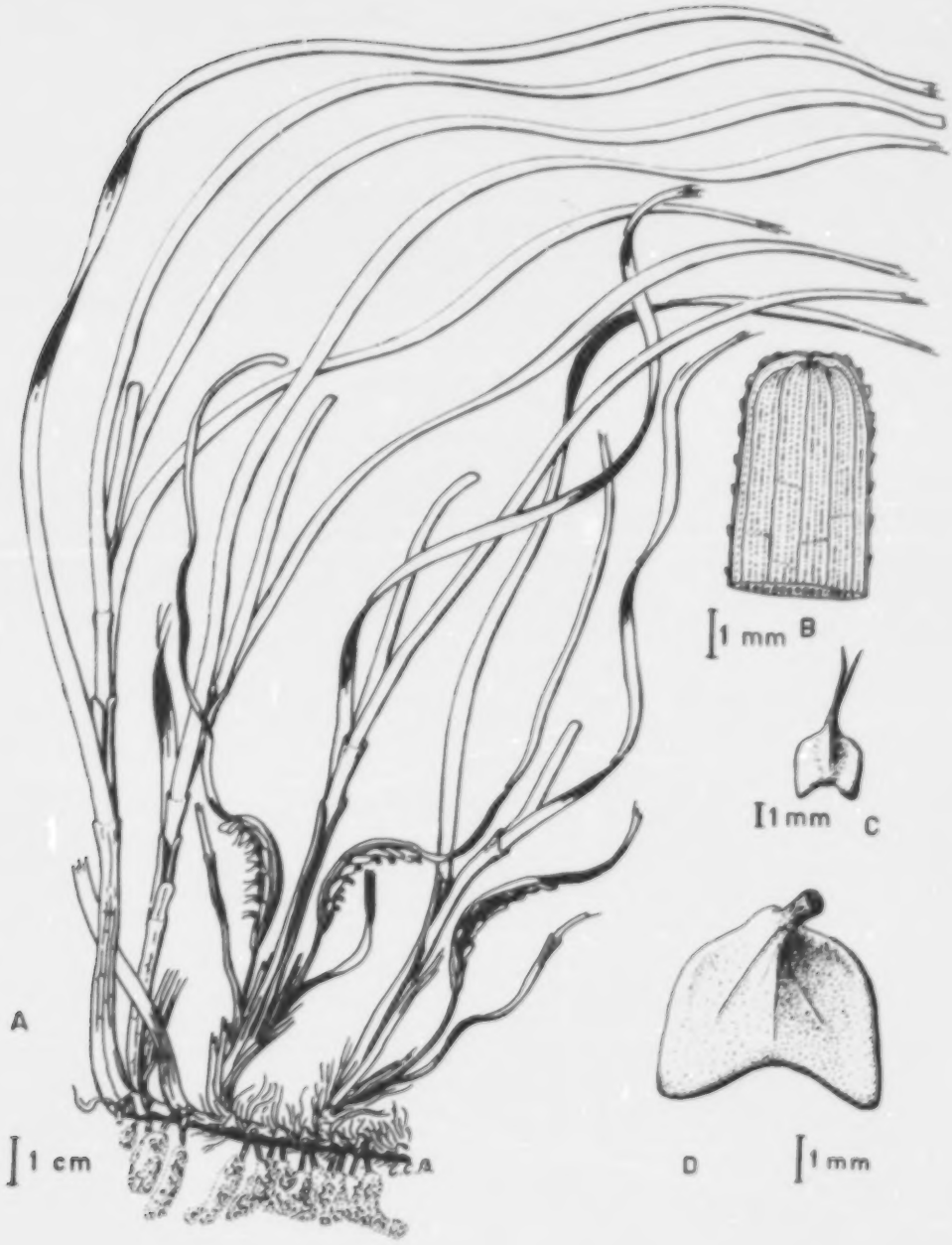


Figure 11. *Phyllospadix serrulatus*: A, pistillate plant; B, leaf tip; C, pistillate flower; D, achene.

The short leafless peduncle normally bears a single spathe, which, on the pistillate plant, contains 5–12 flowers, with very oblique tepals.

This species is often not distinguished from *P. scouleri;* and collections of that species often contain mixed material. Our least common species of this genus, it is seldom found in flower or fruit.

This species ranges from Oregon to southwestern Alaska. Its ecological range is still poorly understood, at least on this coast. Local material around Victoria has been found in more sheltered rock pools and similar habitats, extending higher than, but overlapping the range of *P. scouleri* in the intertidal zone. Pistillate plants appear to be much more abundant than staminate plants (*see* map p. 133).

***Phyllospadix torreyi* Watson**

Rhizome rather more uniform in thickness than that of *P. scouleri*, but otherwise similar. Fertile stems slender, often elongating to a metre or more in length, and bearing frequent branches. Sterile shoots stemless.

Leaves generally very slender; 1.5–2.5 mm wide, narrower than in *P. scouleri*, on the average. Lacunae, when developed, tending to be in two layers.

Spathes several or many, one or commonly two arising from a node in the stem, terminating short axillary branches. Each spathe contains 14–20 flowers.

Apparently scarcer with us than *P. scouleri*, this species is mainly distributed from Oregon to Baja California. The author found it commoner than *P. scouleri* at Triangle Island, where it was growing in rock pools with sandy bottoms, while *P. scouleri* and *P. serrulatus* were confined to pools where they could attach directly to the rock. Our northernmost records are from Calvert Island. This species occurs on the most exposed parts of the coast, appearing to avoid the more sheltered waters of the Strait of Georgia and adjacent straits; and characteristically grows deeper into the subtidal waters than *P. scouleri* (Phillips, 1979) (*see* map p. 134).

The Genus *ZOSTERA* L.

Eel-grass, Grass-wrack

Monoicous perennials with smooth rhizomes of uniform thickness, rooting at the nodes, and giving rise to shoots of two kinds. Purely vegetative shoots short-stemmed or stemless, with ribbon-like, 3- to many-veined leaves rounded or emarginate at the tips, and with lacunae occupying more than half the leaf-thickness. Axillary scales usually 2.

Fertile shoots with flattened stems and supra-axillary branching, prophylls with short blades or reduced to sheaths, and leaf-like bracts with blades that are shorter and narrower than the leaves of vegetative shoots. Spadix with or without minute infra-marginal tepals. Flowers alternating in two rows on one side of the flat spadix. According to one interpretation of the structure, the anthers and ovaries comprise distinct, unisexual flowers; according to another interpretation, a flower comprises one anther, of two anther-sacs, and the ovary next to it, plus, when present, the tepal adjacent to the anther. The ovary is attached at its mid-point, has a style and two linear stigmas. Fruit is an ellipsoid utricle, attached at mid-length, rounded at the base and with an apical stylar beak. Seed one, smooth or longitudinally ribbed.

KEY TO SPECIES

1. **a.** Leaf sheaths on sterile shoots closed at base. Leaves 1.5–12 mm wide, 5- to many-veined, rounded at tips. Spadix without infra-marginal tepals or with a pair at base ..... ***Z. marina***
   b. All leaf sheaths split to base. Leaves 1–1.5 mm wide, 3-veined, rounded or emarginate at tips. Spadix with minute infra-marginal tepals beside the anthers ..... ***Z. japonica***

Our species of *Zostera* are generally found in more sheltered waters than *Phyllospadix*, and have their rhizomes and roots buried in sediment rather than attached to rock.

***Zostera japonica* Ascherson and Graebner**
***Z. americana* Den Hartog, for North American plants**

Small, very slender plant with filiform rhizomes and flowering stems, and short-stemmed or stemless vegetative shoots.

Leaves 1–3 dm long and 1–1½ mm wide, with rounded or slightly notched tips, and with three longitudinal veins, the lateral two marginal; all leaf sheaths opaque and split to the bases. The leaves soon become abraded at their tips, the first effect appearing as a notch in the initially rounded apex.

Figure 12. *Phyllospadix torreyi*: A, pistillate plant with flowers (above) and fruit; B, pistillate flower; C, achene.

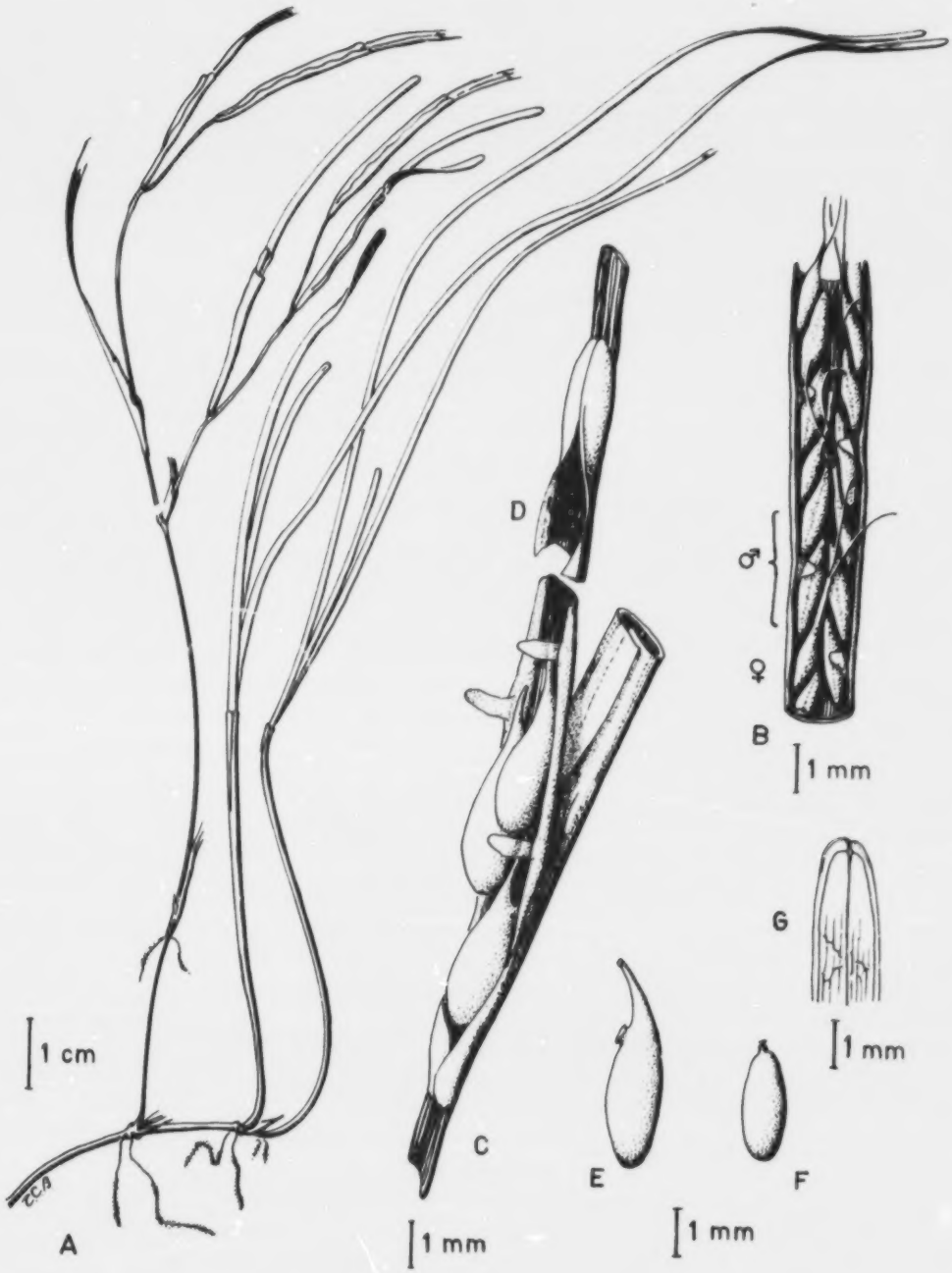


Figure 13. *Zostera japonica*: A, plant; B, segment of spadix with staminate and pistillate flowers; C, base of spathe and spadix, with fruit; D, upper part of spathe sheath; E, fruit (utricle); F, seed; G, leaf tip.

Only the youngest leaves have entire, rounded apices; therefore, the use of this distinction in leaf tips as a diagnostic character for the species is regarded as very unsafe.

Fertile shoots lateral on the rhizome. Spadix with minute (1–1½ mm long) ovate to deltoid tepals arising just within the margin adjacent to the anthers. Fruit about 2 mm long, it and the seed without longitudinal ribs.

The true identity of this plant is still a matter of debate. The tepals are generally narrower and less obviously deltoid than those of typical *Z. japonica;* but still appear nearer to that than to the European *Z. noltei* Hornemann [*Z. minor* (Cavolini) Nolte, *nomen invalidum*, *Z. nana* Mertens ex Roth, *nomen illegitimum*)] with which our plant has also been identified, but which has more elongated, narrow-based, lanceolate tepals (Yuzepchuk, 1934; Harrison, 1976).

As the eastern Asiatic *Z. japonica*, this plant is suspected of having been introduced with oysters from Japan. It is now found abundantly in Boundary Bay, and at Tsawwassen, as well as at several points on the coast of the State of Washington. It occurs in silty or muddy areas, higher in the intertidal zone than *Z. marina*. At Tsawwassen, the author found it above the mid-tide level, where it appears to be invading a colony of the alga *Ulva;* while at Crescent Beach it dominates appreciable areas of the tidal mud-banks (*see* map p. 134).

***Zostera marina* L.** **Eel-grass, Grass-wrack**

***Z. angustifolia* (Hornemann) Reichenback (in part), *Z. hornemanniana* Tutin,**

***Z. stenophylla* Rafinesque = *Z. marina* var. *stenophylla* (Rafinesque) Ascherson and Graebner**

***Z. pacifica* S. Watson = *Z. marina* var. *latifolia* Morong**

Coarse perennial with stout smooth rhizomes, and stemless sterile shoots.

Leaves variable but generally coarse; on vegetative shoots often over a metre long and 1½–12 mm wide, with rounded tips, and with 3–11 veins, the outermost veins inframarginal; the sheaths of vegetative leaves closed, flattened-tubular, closely enclosing the shoot, and translucent ventrally.

Fertile shoots terminal on the rhizomes, long-stemmed, up to 2 metres or more long, with supra-axillary branches and with leaves shorter and narrower than those of the sterile shoots. Prophylls with or without short blades. Sheaths of the leaf-like bracts (spathes) open to base, with firm, opaque margins. Spadix without tepals or with one each side beside the lowest anther.

At flowering time the two elongate tapering stigmas of the pistillate flowers project from between the overlapping margins of the spathe. The pistillate flowers are receptive before the anthers in the same spathe are ripe; and the stigmas are shed by the time the pollen of adjacent anthers is discharged. Pollen grains are thread-like and up to 3 mm long. They are discharged into the water in clouds from ripe inflorescences, and are carried away on the water currents, to entangle with the stigmas of receptive pistillate flowers. The fruit is a utricle, 5–8 mm long, centrally attached, with a horn-like projection (the stylar beak) at one end; the utricle ultimately rupturing to expose the seed, which is 2½–4 mm long, and longitudinally ribbed. Fruiting shoots ultimately become detached and drift away (*see* map p. 135).

KEY TO VARIETIES

1. **a.** Leaves of sterile shoots 1–6 mm wide, opaque, with 3 or sometimes 5 veins. Stems filiform ..... var. ***stenophylla***
   b. Leaves of sterile shoots 4–12 mm wide, with 5–11 veins, rather translucent. Stems robust 2

2. **a.** Leaves of sterile shoots 4–10 mm wide, with 5–7 veins ..... var. ***marina***
   b. Leaves of sterile shoots 10–12 mm wide, with 7–11 veins, translucent ..... var. ***latifolia***

Widely distributed along sea coasts of the Northern Hemisphere, *Zostera marina* often forms extensive meadow-like colonies in sheltered lagoons and bays. It roots in a bottom of coarse or fine sediment, seldom being found on rocks. The base of the plant is usually permanently submerged, sometimes by a few metres.

It has been suspected, but not demonstrated, that the above varieties represent merely individual responses to variation in such environmental factors as water temperature or degree of shelter or exposure (Den Hartog, 1970).

Variety *stenophylla* (Rafinesque) Ascherson and Graebner (? *Z. angustifolia* (Hornemann) Reichenbach, *Z. hornemanniana* Tutin) is recorded from the Queen Charlotte Islands, from Nanoose Bay, Vancouver Island, Boundary Bay and from Savary Island. It appears to be intertidal in

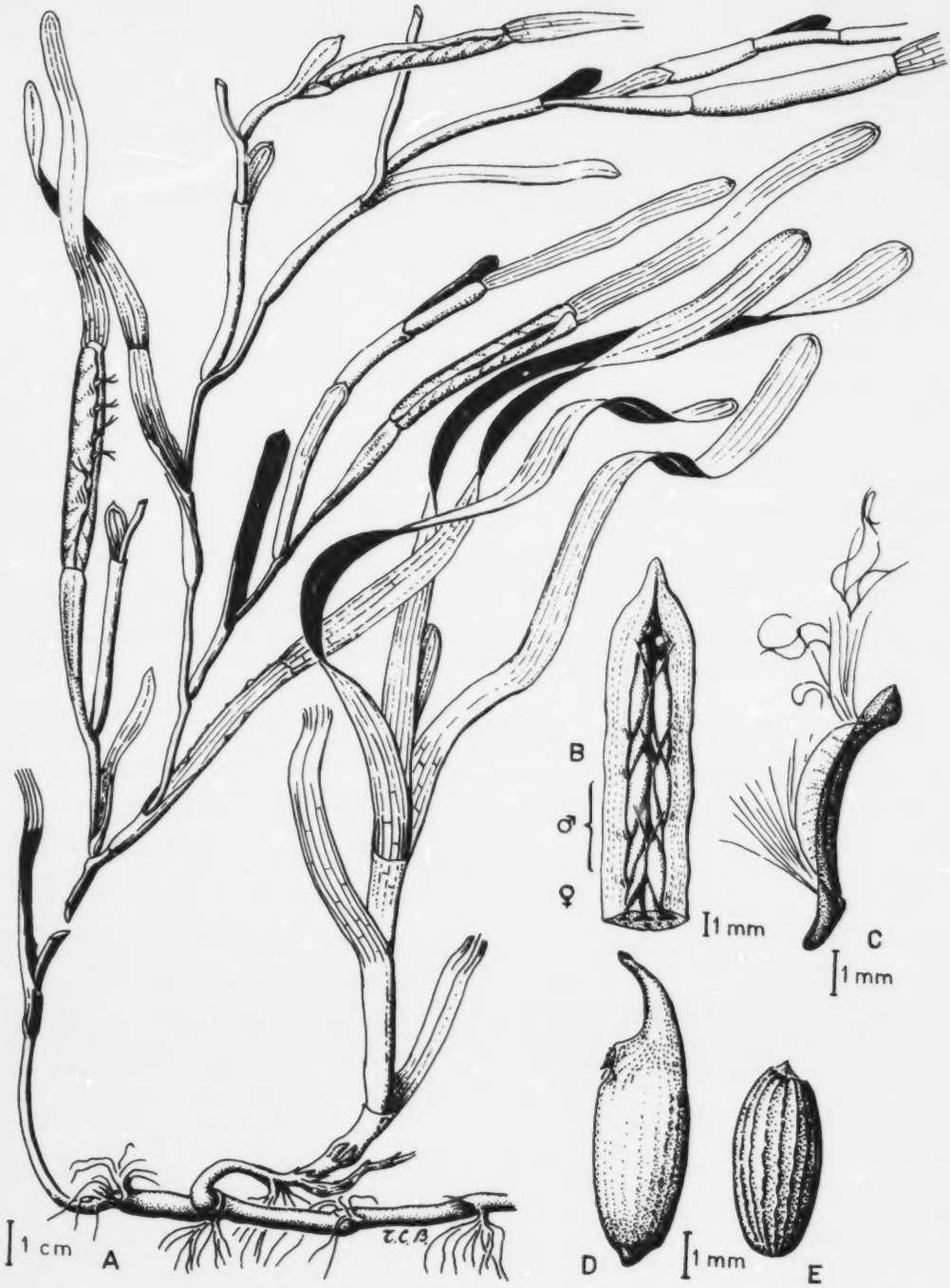


Figure 14. *Zostera marina*: A, plant; B, upper part of spadix, with staminate and pistillate flowers; C, anther shedding pollen; D, fruit (utricle); E, seed.

distribution, though ecological information with specimens examined by the author is too sparse to confirm this absolutely. Variety *latifolia* Morong (*Z. pacifica* S. Watson), found in sheltered waters, in Sooke Basin and Bamfield Harbour, is subtidal, only the upper parts of the plants reaching the surface. It occurs on the Pacific coast of North America from southern British Columbia to California. An annual form, lacking vegetative shoots, has been reported from the Atlantic coast of this continent, but has not been found yet on the Pacific coast.

The Family ALISMATACEAE (Alismaceae)

Water-plantain Family

Annuals or perennials with basal leaf rosettes and terminal cymose inflorescences of peculiar structure.

The earliest leaves produced are ribbon-like, without broad, expanded blades. Later leaves usually have broad blades.

Branching in the inflorescence is basically alternate, with one bract, prophyll, or branch at each node; but in the main axis, the failure of two out of every three internodes to elongate during growth results in the formation of whorl-like aggregates (false whorls) of bracts, and umbel-like clusters (false umbels) of branches (Charlton, 1973). Flowers bisexual or unisexual, sepals and petals differentiated, the latter often showy. Stamens 6 or more and, when more, originating in clusters opposite the petals. Carpels 6 to many, originating in rough whorls or clusters, not spirally arranged; separate, in fruit becoming achenes, or rarely, 2-seeded follicles. Seeds with horseshoe-shaped embryos and no endosperm.

A worldwide family of 13 genera, clearly related to the Butomaceae. Some members of this family are highly plastic in their response to vagaries in the environment. After the development of the juvenile ribbon-like leaves, the likelihood of later leaves producing broad blades varies from species to species, and may be modified by the environment. In some species, such as *Alisma gramineum* and *Sagittaria cuneata*, deep submergence in mid to late summer may induce retention of, or a return to, the juvenile foliage form, with suppression of the expanded blade (Arber, 1920).

KEY TO GENERA IN BRITISH COLUMBIA

1. a. Flowers bisexual, small. Carpels whorled. Terminal flower present ..... ***Alisma***
b. Flowers unisexual, often showy. Carpels very many in a head. Terminal flower absent ..... ***Sagittaria***

The Genus *ALISMA* L.

Water-plantain

Perennial herbs with rosettes of basal leaves and terminal panicles of flowers. Extension of vegetative growth from axillary buds produces leafy rosettes that in favourable conditions may terminate in secondary panicles the same year. Stolons or rhizomes as seen in *Sagittaria* are not produced.

Flowers occur in cymose panicles made up of false whorls, each with three bracts and a number of axillary scales. In the axil of each bract a lateral branch arises. Each branch bears at its base a bract-like, 2-toothed prophyll in the angle between the branch and the main axis. Branching from the axils of the basal and more distal prophylls increases the number of flowers originating from the axil of each bract in the axial whorl. The panicle ends in a terminal flower.

Each flower consists of 3 sepals, 3 white, or occasionally pink, petals, 6 stamens, 2 opposite each petal, and 10–25 separate carpels in a whorl. The margins of each carpel are pressed together, but not united, at flowering time (Singh and Sattler, 1972). The fruit is a whorl of achenes.

KEY TO SPECIES

1. a. Leaves of mature plant emergent, with broadly oval blades and semiterete, channeled, stiff petioles. Panicle longer than the leaves. Petals about twice as long as the sepals ..... ***A. plantago-aquatica***
b. Leaves usually submerged or floating, and narrowly ribbon-like, but sometimes emergent with small lanceolate blades and flattened petioles. Panicle usually shorter than the longest leaves. Petals shorter than to slightly longer than the sepals ..... ***A. gramineum***

***Alisma gramineum* Lejeune** **Narrow-leaved Water-plaintain**

***A. geyeri* Torrey**

***A. plantago* var. *angustissimum* DC. = *A. gramineum* var. *angustissimum* (DC.) Hendricks**

Leaves typically narrowly ribbon-like, floating or submerged, flaccid and trailing; but sometimes, with water levels fluctuating or declining in late summer, producing stiff, emergent leaves with small lanceolate blades.

Panicle usually shorter than the longest leaves, with 2 to 5 nodes, erect or the axis and branches tending to curve downward.

Flowers small, 3–4 mm wide, the white to pink petals shorter than to barely longer than the green sepals. Anthers nearly round. Carpels with recurved styles. Achenes with two or more dorsal grooves and a curved beak up to 0.5 mm long (*see* map p. 135).

KEY TO VARIETIES

1. **a.** Leaves mainly submerged or floating, linear and ribbon-like, or with narrow lanceolate blades up to 5 mm wide. Panicle axis, branches and pedicels tending to curve downward ..... var. ***gramineum***
   b. Leaves usually erect and emergent, with lanceolate blades 5–20 (rarely to 40) mm wide. Panicle erect ..... var. ***angustissimum***

Our two varieties differ strikingly in appearance but it is uncertain how much of the diversity is genetic in origin, and how much is due to the varying response of a very plastic species to varying depths of water or to cycles of flooding and emergence.

A plant of marshes, sometimes within the uppermost tidal range, or completely submerged in lakes or rivers, this species has been found flowering a metre beneath the surface of the upper Columbia River. Widespread in the Northern Hemisphere, it is seldom recorded in British Columbia. However, its scarcity may be more apparent than real, as it is easily overlooked in marsh vegetation, or when deeply submerged. Our only records of var. *angustissimum* (DC.) Hendricks are from west of the Coast Range, while var. *gramineum* is found in the interior.

***Alisma plantago-aquatica* L.** **Water-plantain**

***A. triviale* Pursh = *A. plantago-aquatica* L. var. *americanum* Schultes and Schultes**

Erect plant, when mature with rosettes of upstanding leaves with elliptic, rarely lanceolate blades 3–15 cm wide, cordate, cuneate or rounded at base, on semi-terete channeled petioles.

Panicle stiffly erect, taller than the leaves, with 4–8 false whorls of bracts and branches. Flowers 6–9 mm wide when fully open, larger than in *A. gramineum*, opening wide. Petals twice as long as the sepals, and white, or sometimes pink. Anthers twice as long as thick. Styles straight or curved, usually arising high on the inner margins of the carpels.

Achene with one or two dorsal grooves, and usually a straight beak (*see* map p. 136).

KEY TO VARIETIES

1. **a.** Petals predominantly white. Leaf blade elliptic, cordate to rounded at base. Style subterminally attached to ovary, curved at flowering time ..... var. ***americanum***
   b. Petals pink. Leaf blade lanceolate, cuneate to cordate at base. Style laterally attached to ovary, straight at flowering time ..... var. ***plantago-aquatica***

Variety *plantago-aquatica* is the typical variety in Eurasia, and occasionally has been recorded as an introduced plant in North America. The North American var. *americanum* Schultes and Schultes (*A. triviale* Pursh) is typically white flowered, but plants with pink petals occur sporadically throughout our area. However, this characteristic is not closely correlated with the other characteristics defining var. *plantago-aquatica*, though they may on occasion occur in the same plant.

Usually a plant of muddy ditches and marshes, seldom in deep water, and never completely submerged; this species is of nearly worldwide distribution.

The Genus *SAGITTARIA* L.

Arrowhead

Perennial herbs with rosettes of leaves and terminal panicles of flowers. Extension of vegetative growth is from axillary buds that give rise to slender rhizomes or stolons that may terminate in overwintering starchy tubers.

Figure 15. *Alisma gramineum* var. *angustissimum*: A, plant; B, flower; C, fruiting flower (whorl of achenes); D, achene.

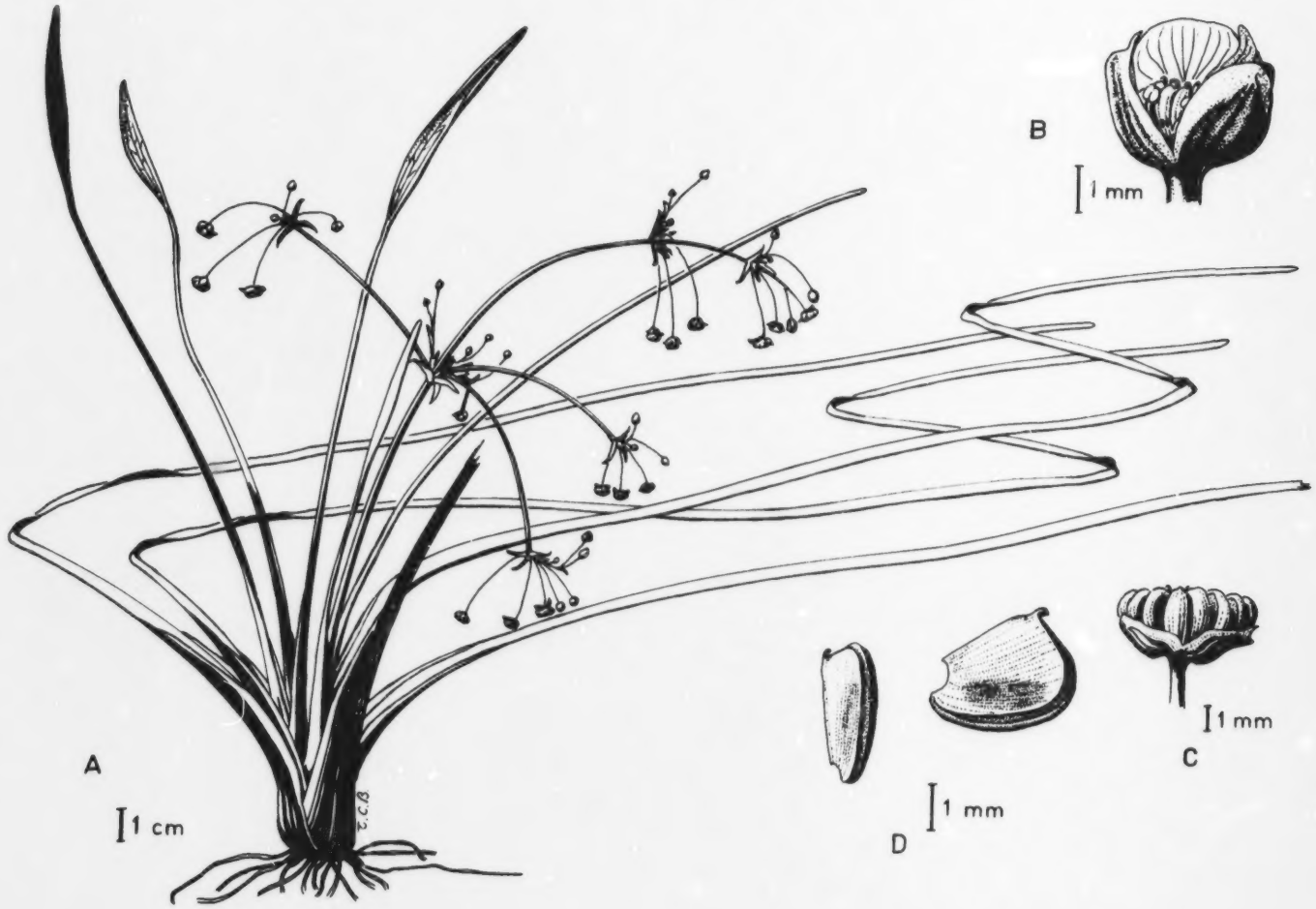


Figure 16. *Alisma gramineum* var. *gramineum*: A, plant; B, flower, with nearest petal removed; C, fruit (whorl of achenes); D, achenes.

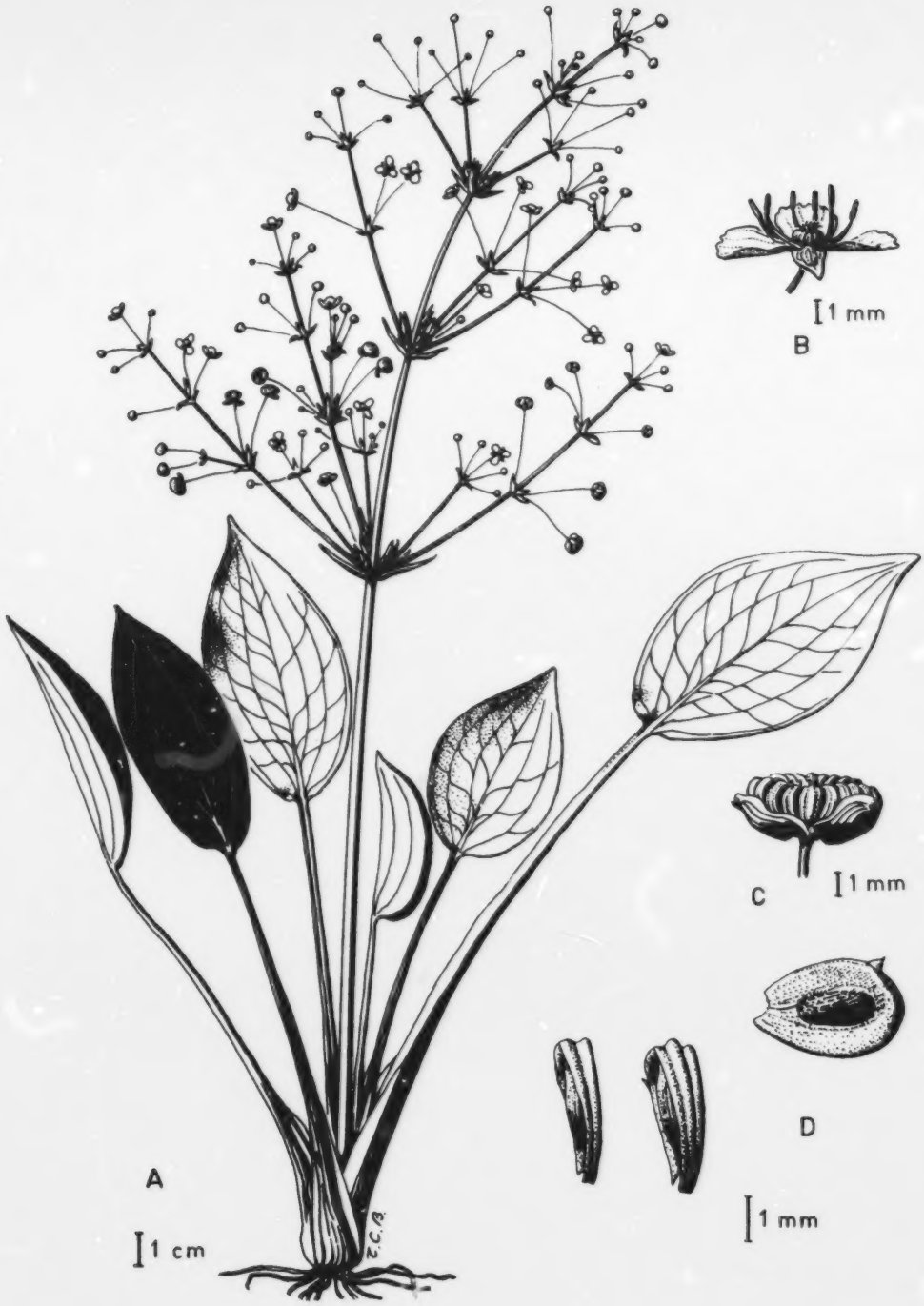


Figure 17. *Alisma plantago-aquatica*: A, plant; B, flower; C, fruiting flower (whorl of achenes); D, achenes.

Inflorescence a panicle or raceme, with bracts and axillary pedicels in false whorls of three. Prophylls and their axillary branchlets are not normally produced, and lateral branches bearing more than one flower are seldom found. There is no terminal flower.

Flowers are of two kinds: staminate flowers occupying the upper part of an inflorescence, and pistillate flowers the lower part. Occasionally plants are found that are entirely staminate or pistillate. Each flower has three sepals and three relatively large white petals. Staminate flowers produce many stamens; the outer in pairs opposite the petals, the inner whorls alternating with the outer ones; and a number of abortive carpels. Pistillate flowers have several staminodes (sterile, abortive stamens) and many carpels in rough whorls, forming a globose head; each carpel with closed and united margins and with a short style and stigma (Singh and Sattler, 1973). The fruit is a globose head of many flattish achenes, each with a short flattened stylar beak.

KEY TO SPECIES

1. **a.** Living petioles usually angular in cross-section. Pedicels of equal length. Bracts ovate, rounded or hooded at tips, up to 10 mm long. Achenes with longish oblique beaks. ..... ***S. latifolia***
   b. Living petioles usually rounded in cross-section. Pistillate pedicels shorter than staminate pedicel. Bracts lanceolate, acuminate, up to 30 mm long. Achenes with short, apically protruding beaks. ..... ***S. cuneata***

Where abundant, members of this genus may be important wildlife food plants. The tubers are eaten by muskrats and other rodents (Fassett, 1940) and, if not too big, by waterfowl. Upper plant parts are also eaten.

Sagittaria cuneata Sheldon
S. arifolia Nuttall

Perennial, spreading by slender rhizomes. Leaf form exceedingly plastic, varying in response to depth of water and other influences. Early leaves reduced to tapering flattened petioles without blades; later leaves with usually rounded petioles when alive, floating, or emergent and erect with sagittate blades with narrow or broad lobes, or occasionally ovate and lacking the basal lobes. In deep water the plant develops very long filiform petioles and very small floating ovate blades.

Inflorescence a raceme, with lanceolate, acuminate bracts up to 30 mm long. Staminate pedicels about twice as long as pistillate ones. Petals twice as long as sepals.

Achene 2.5–4 mm long, with an apical beak 0.2–0.5 mm long, projecting in line with the axis of the achene; pronounced dorsal and ventral keels that are almost wing-like, and a rather translucent wall over the locule through which the enclosed embryo, closely invested by the seed coat, can be distinguished by the aid of a microscope.

Distributed widely across temperate North America, from California to northern Canada, this is the commoner and more widespread species of *Sagittaria* in this province. It is found in ditches and in sheltered or even open water up to 1½ metres deep, where the leaves and flowers may barely reach the surface. It has not been seen by the author to flower in water more than a metre deep (*see* map p. 136).

Sagittaria latifolia Willdenow — **Wapato**

Perennial, spreading by slender rhizomes often ending in tubers. Leaves apparently less plastic in form than those of *S. cuneata;* mature plant normally with erect sagittate blades with lobes of varying width, on petioles that are angular in cross-section when alive.

Monoicous or occasionally dioicous. The inflorescence appears more slender than that of *S. cuneata*, due to the shorter staminate pedicels, which are no longer than the pistillate ones. Peduncle triangular in cross-section. Bracts 5–10 mm long, rounded or hooded at tips. Petals twice as long as sepals.

Achene 3–5 mm long, with an oblique beak, 0.5–1.5 mm long, turned toward the apex of the flower axis.

Widespread in the Americas, this species is uncommon with us. Growing in marshes and sheltered shallow waters, this species is not seen in as deep water as is *S. cuneata* (*see* map p. 137).

Figure 18. *Sagittaria cuneata*: A, plant, with staminate flowers open, pistillate flowers at fruiting stage; B, achene.

Figure 19. *Sagittaria latifolia*: A, plant, with pistillate flowers open; B, staminate flower; C, head of achenes; D, achene; E, tuber.

The Family JUNCAGINACEAE

Arrow-grass Family

Rush-like marsh plants with erect basal rosettes of terete or rather flattened linear leaves with sheathing bases.

Flowers mainly in spikes or racemes (some axillary), minute, with or without bracts or perianths. Stamens 1–6; carpels 1–6, connate, with one ovule per carpel.

KEY TO GENERA

1. **a.** Flowers in bractless racemes, all complete, with 6 perianth parts (tepals), and 3 or 6 carpels. Fruit a schizocarp ***Triglochin***
   b. Perfect flowers in minutely bracted spikes, and consisting of one stamen and one carpel. Pistillate flowers in basal leaf sheaths, long-styled. Fruit an achene ***Lilaea***

The Genus *LILAEA* Humboldt & Bonpland

Flowering Quillwort

Annual with terete leaves with ample basal sheaths, and with flowers and pedunculate spikes arising in the leaf axils.

Flowers of three kinds: (a) perfect (bisexual) flowers in the lower spike, each flower with a minute bract (interpreted by some as a vestigial tepal), one stamen, and one carpel with a short style and a capitate stigma; (b) pistillate flowers solitary in the basal leaf sheaths, and having apparently 3 fused carpels and a very long style emerging from the leaf sheaths and terminating in a capitate and rather plumose stigma; and (c) staminate flowers with a caducous bract and a subsessile, 2-celled anther, near the spike apex. Fruit is an achene, those of the basal flowers with 3 small projections at the top.

***Lilaea scilloides* (Poiret) Haumann**
***L. subulata* Humboldt & Bonpland**

The only species. Widespread in the Americas but seldom collected; found in shallow waters in alkaline, saline or brackish marshes (*see* map p. 137).

The Genus *TRIGLOCHIN* L.

Arrow-grass

Marsh-inhabiting perennials with short rhizomes and erect leaf rosettes.

Flowers all alike and bisexual, in terminal bractless spike-like racemes sometimes appearing lateral by reason of extension of vegetative growth from axillary buds. Each flower with 6 similar tepals, 6 stamens, and 3 or 6 connate carpels; each carpel containing one erect ovule. Stigmas sessile, rather plumose. Fruit a schizocarp, the carpels at maturity splitting away from each other and from the central axis of the flower, and each containing one seed.

Triglochin maritimum and *T. palustre* are well-known causes of livestock poisoning the toxic effect being due to hydrocyanic acid.

KEY TO SPECIES

1. **a.** Carpels and stigmas 3. Fruit linear or slenderly club-shaped; splitting from a 3-winged floral axis. Ligule divided ***T. palustre***
   b. Carpels and stigmas 6. Fruit ovoid; splitting from a terete floral axis 2
2. **a.** Ligule entire or nearly so, 1.5–5 mm long. Plant 2 dm tall or more. Leaf blade ± flattened. Raceme usually taller than leaves ***T. maritimum***
   b. Ligule divided, 0.3–1 mm long. Plant shorter. Leaf blade almost terete. Raceme usually shorter than leaves ***T. concinnum***

***Triglochin concinnum* Davey**

Small slender plant with a slender rhizome, relatively short, semi-terete, blunt-tipped leaves, and a ligule notched or divided at the top.

Raceme relatively short and few-flowered (5–20 flowers), often shorter than the leaves. Flower minute (about 1.5 mm wide and high at pollinating time), with 6 tepals, 6 stamens, and 6 carpels. Fruit similar to that of *T. maritimum*, the 6 carpels splitting from the cylindrical floral axis and from each other longitudinally.

Figure 20. *Lilaea scilloides*: A, plant; B, perfect flower, from spike; C, fruit (achene) from spike; D, basal axillary fruit.

Figure 21. *Triglochin concinnum*: A, fruiting plant; B, fruit (6 achenes); C, achene separating from floral axis.

Our variety is the typical var. *concinnum*, which occurs along the coast from British Columbia south to Baja California. It is found uncommonly in tidal marshes. In British Columbia it has so far been found at Sidney, South Pender Island, and Graham Island in the Queen Charlotte Islands. Being a relatively inconspicuous plant, it may go unnoticed when growing among its taller relative, *T. maritimum*; and may in fact be more frequent in occurrence than the existing collections suggest (*see* map p. 138).

***Triglochin maritimum* L.**

Taller and stouter than the other species of this genus: 20–120 cm tall; with a stout rhizome often covered with the fibrous remnants of old leaf bases. Leaf blade semi-terete to rather flattened. Ligule entire and acute or rounded at the top.

Flowers 3–4 mm wide and high, many in a long raceme usually well over-topping the foliage, opening progressively from base to apex, but the fruits ripening nearly simultaneously. Carpels 6 (occasionally 3), 3 of their stigmas often more prominent than the rest. Fruit splitting lengthwise into 6 carpels that separate from the cylindrical floral axis.

Widespread in the Americas and Eurasia. Common in tidal marshes along the coast, and around brackish or alkaline ponds and seeps in the interior; sometimes forming large clumps. Our commonest species of this genus (*see* map p. 138).

***Triglochin palustre* L.**

Slender plant with a short weak rhizome, and filiform, terete or semi-terete leaves flattened or channeled on the ventral or upper side. Ligule (sheath projection) divided at the top.

Inflorescence a very slender, open, terminal or apparently axillary, bractless raceme, the peduncle often somewhat flattened when young. Flower minute (about 2 mm wide and high at pollinating time), and consisting of 6 tepals, with a stamen opposite, and basally adherent to, each tepal, and 3 carpels coherent into an ovary crowned by the sessile, brush-like stigmas.

Fruit a slender schizocarp, splitting into three 1-seeded carpels, separating from the winged floral axis progressively upward from the base.

Widespread in the Americas and Eurasia; in saline, brackish, or alkaline marshes or seasonally moist meadows (*see* map p. 139).

The Family POTAMOGETONACEAE

Pondweed Family

Perennials, usually with slender submerged rhizomes or stolons, slender pliable stems that are submerged except often for the inflorescence, alternate or sometimes subopposite leaves, and stipular sheaths or ligules.

The inflorescence is a terminal spike with 2 to many perfect flowers; each flower with 2 or 4 stamens, each adnate to an appendage that is variously interpreted as a tepal or a stamen connective, and usually 4 separate carpels, each with a terminal stigma and containing one curved ovule. In fruit, each carpel develops into an achene, sometimes rather drupe-like by reason of a spongy or fleshy outer wall, with a stigma that may be sessile or raised on a stylar beak, and containing a curved or coiled embryo and no endosperm.

The family, as treated now, contains 5 genera, two of which are represented in British Columbia.

KEY TO GENERA IN BRITISH COLUMBIA

1. **a.** Spike with 2 flowers. Stamens and tepals 2 per flower. Achenes with long stipes — ***Ruppia***
   b. Spike with 4 to many flowers. Stamens and tepals 4 per flower. Achenes ± sessile — ***Potamogeton***

The Genus *POTAMOGETON* L.

Pondweeds

Soft-stemmed aquatic perennials of diverse aspect: totally submerged or with the inflorescence emergent and the uppermost leaves floating. Leaves alternate and 2-ranked, or appearing subopposite under an inflorescence, as the distal stem internode fails to elongate. Totally submersed plants generally have leaves of uniform type: thin, usually sessile, and often translucent; but in species with floating as well as submersed foliage, the leaves in these situations differ strikingly in character. The floating leaves generally have longer petioles, and broader, thicker, opaque blades with more

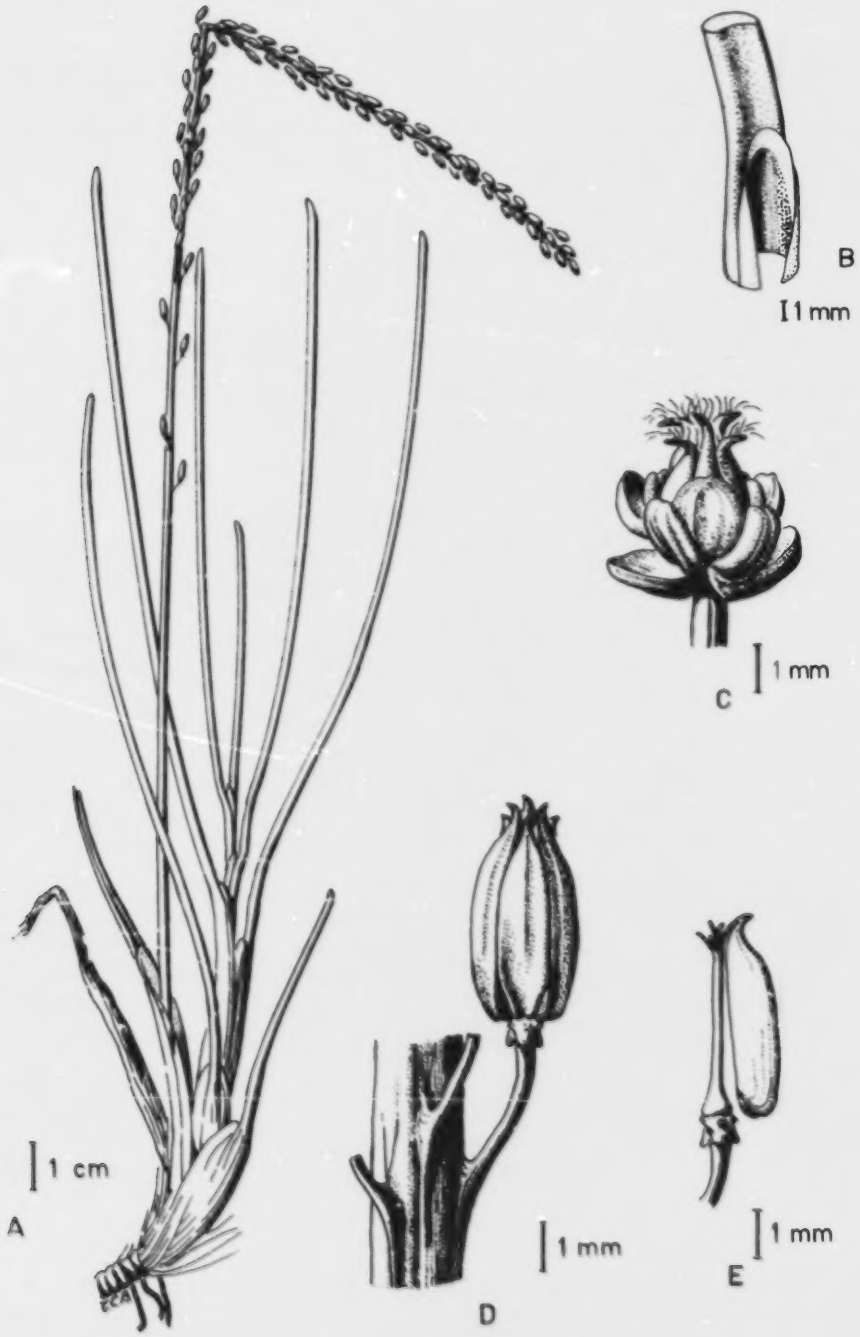


Figure 22. *Triglochin maritimum*: A, small fruiting plant; B, leaf base and ligule; C, flower; D, fruit cluster (6 achenes) from one flower; E, achene separating from floral axis.

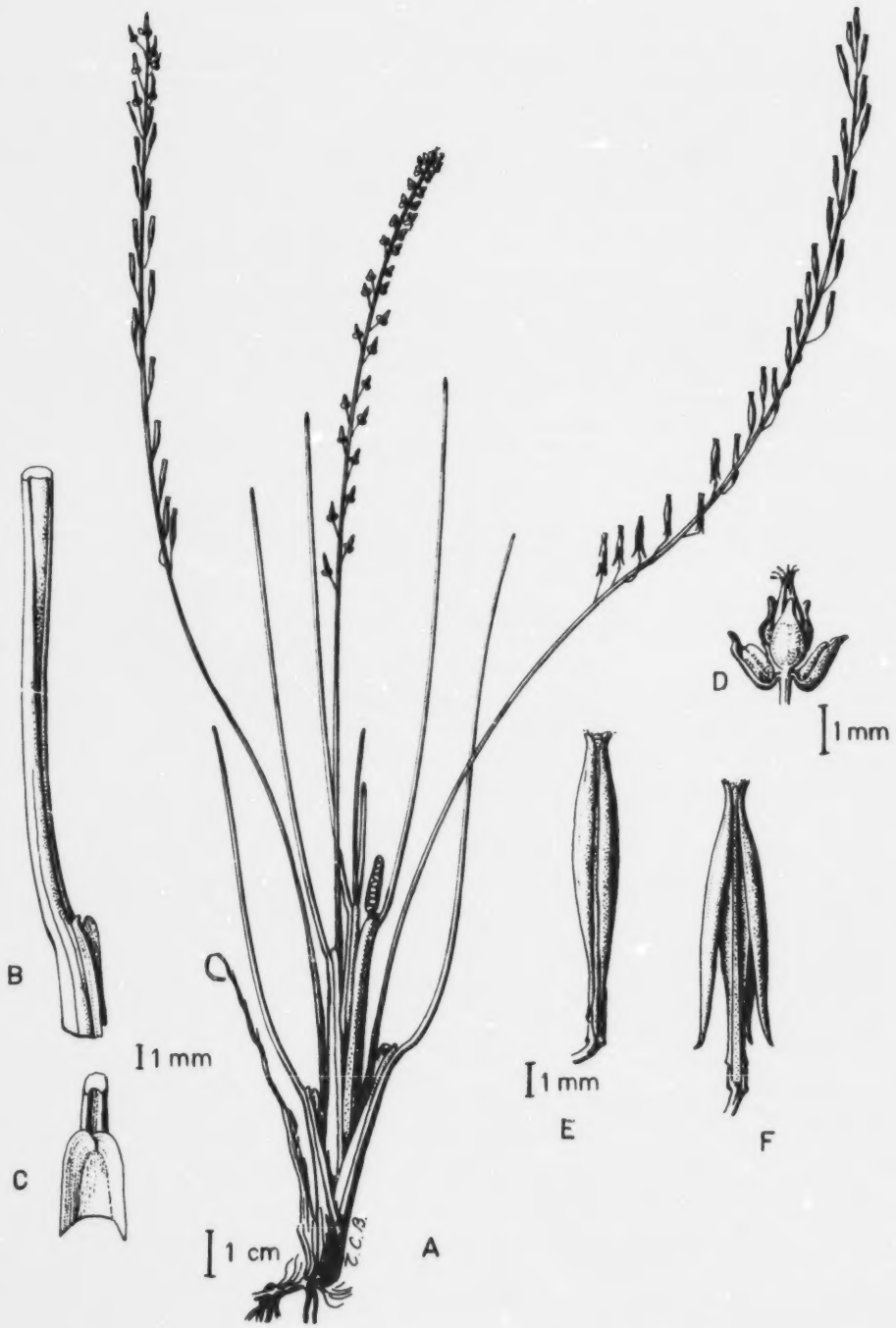


Figure 23. *Triglochin palustre*: A, plant; B, leaf base and divided ligule (side view); C, leaf base and divided ligule (face view); D, flower; E, fruit cluster (3 achenes) from one flower; F, achenes separating from floral axis.

longitudinal veins than have the submersed leaves. Transitional leaf forms sometimes occur. The stipular sheaths or ligules are usually conspicuous, and their varied character is of diagnostic importance.

Spike with 4 to many flowers in irregular whorls or pairs, each flower with 4 tepals, to each of which is adnate a sessile anther of 2 anther sacs, and usually 4 separate sessile or subsessile carpels with terminal stigmas. Fruit a more or less sessile, often fleshy-walled achene, containing a U-shaped or coiled embryo, whose form is often distinguishable through distension of the outer layers of the fruit.

Potamogeton is a genus of about 100 species, of cosmopolitan range, but principally of north temperate latitudes. About 40 species are indigenous to North America; 22 in British Columbia. The plants generally occur in still or slowly flowing fresh waters; however, a few species, such as *P. filiformis* and *P. pectinatus*, are sometimes found in brackish or saline waters of tidal marshes.

Most species produce, in the bottom sediments beneath the water, slender horizontal rhizomes which form the principal means of vegetative propagation. The rhizome is formed from the first two internodes of a basal branch, which then turns up to form an upright shoot. Axillary buds at the base of the vertical segment may give rise to rhizome extensions in the same way. Distinct over-wintering tubers are formed on the rhizomes of some species; a typical tuber consisting of two successive, short, swollen internodes.

Many species produce special winter buds, or turions, generally on the upper branches. These are very short branchlets with reduced leaves, and are easily detached. After the plant has decayed in autumn, the winter buds lie on the bed of the water body over winter, sprouting in spring to produce new erect shoots. A few species, such as *P. crispus*, produce both winter buds and rhizomes.

The nomenclature of species in *Potamogeton* is in a most unsatisfactory state. Several of the species and species-complexes have circumboreal ranges, and were first described on the basis of European material in European literature not easily available here. The type specimens, on which the original descriptions were based, are in various European herbaria. Further, since the early nineteenth century at least, the nomenclature applied to species and varities in this genus has to a great degree evolved independently in Europe and North America. The resulting present confusion of names can only be sorted out properly by someone with access to the older European collections and libraries as well as to those in North America.

The nomenclature used in this work is in general conformity with that accepted by most North American botanists as applicable to North American material. However, its precision and correctness are questionable for several species and varieties, including *Potamogeton filiformis*, *P. friesii*, *P. gramineus*, and *P. zosteriformis*.

HYBRIDS IN POTAMOGETON

Hybrids have been recorded between several species in this genus. While of vigorous growth, they are usually sterile. However, their ability to propagate vegetatively from year to year can enable them to establish colonies of long duration and appreciable local extent.

These hybrids, as reported, are putative only. That is to say: they are founded on the examination and interpretation of character combinations in naturally occurring plants. The author is unaware of any attempts to confirm the interpretations by generating the hybrids through artificial cross-breeding experiments with the putative parents.

Only one specific name, normally the oldest, can legitimately be used for the hybrid population between two species, regardless of what varieties or subspecies may have been involved in the parentage. Thus the classification of the parents can affect the choice of names for their hybrid offspring. For example: if *P. perfoliatus* ssp. *richardsonii* is considered as a species [*P. richardsonii* (Bennett) Rydberg] distinct from *P. perfoliatus* L., the hybrids between it and *P. gramineus* L. are properly called *P.* × *hagstroemii* Bennett. If, however, *richardsonii* is combined with *P. perfoliatus* as ssp. *richardsonii* (Bennett) Hulten, then *P.* × *nitens* Weber, the oldest name given to a hybrid between any form of *P. perfoliatus* and *P. gramineus*, is applicable to all such hybrids, including those from ssp. *richardsonii*.

Many hybrids that have been identified in Europe (Dandy and Taylor, 1938–1942) among species of circumboreal distribution are of potential interest here. The following hybrid combinations between parent species occurring in British Columbia have been recorded: those that have been found to date in this province being indicated by asterisks. Where specific names have been applied to the hybrids, they are included.

Potamogeton alpinus × *crispus* = *P.* × *olivaceus* Baagoe ex G. Fischer
P. alpinus × *gramineus* = *P.* × *nericeus* Hagstroem
P. alpinus × *nodosus* = *P.* × *subobtusus* Hagstroem
P. alpinus × *perfoliatus* = *P.* × *prussicus* Hagstroem
P. alpinus × *praelongus* = *P.* × *griffithii* Bennett
* *P. amplifolius* × *illinoensis* = *P.* × *scoliophyllus* Hagstroem
* *P. amplifolius* × *natans*
P. amplifolius × *perfoliatus* ssp. *richardsonii*
* *P. amplifolius* × *praelongus*
P. crispus × *friesii* = *P.* × *lintonii* Fryer
P. crispus × *praelongus* = *P.* × *undulatus* Wolfgang
P. epihydrus × *nodosus* = *P.* × *subsessilis* Hagstroem
P. filiformis × *pectinatus* = *P.* × *suecicus* Richter
* *P. friesii* × *zosteriformis*
* *P. gramineus* × *illinoensis* = *P.* × *spathulaeformis* Morong
P. gramineus × *natans* = *P.* × *sparganifolius* Hagstroem
P. gramineus × *nodosus* = *P.* × *argutulus* Hagstroem
* *P. gramineus* × *perfoliatus* = *P.* × *nitens* Weber
* *P. gramineus* × *perfoliatus* ssp. *richardsonii* (as *P. richardsonii*) = *P.* × *hagstroemii* Bennett
P. illinoensis × *nodosus*
P. illinoensis × *perfoliatus* ssp. *perfoliatus*
P. illinoensis × *perfoliatus* ssp. *richardsonii*
P. natans × *nodous* = *P.* × *perplexus* Bennett
P. nodosus × *perfoliatus* ssp. *richardsonii* = *P.* × *rectifolius* Bennett
P. pectinatus × *vaginatus* = *P.* × *bottnicus* Hagstroem
* *P. perfoliatus* × *praelongus* = *P.* × *cognatus* Ascherson and Graebner

KEY TO SPECIES OF *POTAMOGETON* IN BRITISH COLUMBIA

(Modified from Hitchcock *et al.*: 1969)

1. a. Stipular sheaths adnate to leaf bases, at least of submersed leaves. Submersed leaves linear **2**
b. Sheaths free of leaf bases **6**

2. a. Leaves all alike, submersed, finely serrulate-margined, crowded in 2 ranks, stiff, over 3 mm wide ***P. robbinsii***
b. Leaves entire, less than 3 mm wide, not crowded **3**

3. a. Adnate part of stipular sheath of submersed leaves 5 mm or less long, shorter than free part. Elliptic floating leaves often present ..... ***P. diversifolius***
b. Adnate part of stipular sheath longer, at least as long as free part. Leaves filiform to linear. Floating leaves absent **4**

4. a. Stipular sheaths on main stem dilated, firm, at least some subtending 2, 3, or more branches; the margins separate to base, free tips (ligules) relatively short. Leaf tips rounded. Stigmas sessile ***P. vaginatus***
b. Stipular sheaths slender, subtending one or sometimes 2 branches. Ligules relatively longer. Leaf tips acute **5**

5. a. Stipular sheath margins connate below when young, forming a tubular sheath often later ruptured. Achene beakless, the stigma sessile ..... ***P. filiformis***
b. Sheath margins free to base from the first, though often overlapping. Achene beaked ..... ***P. pectinatus***

6. a. Leaves all submersed and alike in form; oblong, 3–10 mm wide; with margins crispate (closely and regularly undulate) and dentate. Stem flat. Achenes with beaks 2–3 mm long ..... ***P. crispus***
b. Leaves various, but not both crispate and dentate. Achene short-beaked or beakless **7**

7. a. Stem flat, nearly as wide as leaves. Leaves all submersed, linear, with many parallel longitudinal fibres in addition to veins. Carpel one per flower. Achene keeled and beaked ..... ***P. zosteriformis***
b. Stem terete or moderately flattened. Leaves various, but without fibres in addition to veins. Carpels 4 per flower **8**

8. a. Leaves all submersed, cordate and usually clasping at base, usually over 10 mm wide **9**
b. Leaves not cordate or clasping at base **10**

9. a. Stem unbranched or sparingly branched. Leaves usually less than 10 cm long, often recurved, acute or rounded at tips. Peduncle 2–10 cm (rarely more) long. Achene 3–3.5 mm long. Sheaths breaking down into fibres ..... ***P. perfoliatus***

b. Stem profusely branched above, often zigzag. Leaves of various sizes, fascicles of small leaves in axils of leaves 10–20 cm long, rounded and hooded at tips. Peduncle 10–20 cm long. Achenes 4–8 mm long. Sheaths persisting whole ..... ***P. praelongus***

10. a. Stems with paired translucent glands at nodes. All leaves submersed and linear **11**

b. Stems without glands. Leaves various **14**

11. a. Sheaths conspicuous, white, fibrous, breaking down into persistent fibres. Stem flattened **12**

b. Sheaths inconspicuous, membranous, colourless, translucent, non-fibrous, often caducous **13**

12. a. Leaves thin, relatively flaccid, translucent, with 5–7 longitudinal veins, and blunt or rounded tips ..... ***P. friesii***

b. Leaves stiff, opaque, usually 3-veined, with acute tips. Margins often becoming rolled under ..... ***P. strictifolius***

13. a. Leaves 2–3 mm wide, rounded at tips. Achenes 3.5 mm or more long ..... ***P. obtusifolius***

b. Leaves 1–1.5 mm wide, acute at tips. Achenes 2–3 mm long ..... ***P. pusillus***

14. a. Leaves all alike, submersed, small, linear, less than 2 mm wide or 7 cm long **15**

b. Leaves often diverse, either longer or wider, or both. Floating leaves usually present **16**

15. a. Sheath margins connate when young. Achene prominently keeled and beaked ..... ***P. foliosus***

b. Sheath margins free from the first. Achene keel-less, short-beaked ..... ***P. pusillus***

16. a. Submersed leaves narrowly linear, up to 2 mm wide **17**

b. Submersed leaves tapering to ends, 3 mm or more wide **18**

17. a. Stem 1–2 mm thick, unbranched or sparingly branched. Floating leaf 4–12 cm long by 2–6 cm wide, commonly cordate at base and rounded at tip, on a petiole 1–2 mm thick. Submersed leaf stiff, 10–20 cm long ..... ***P. natans***

b. Stem ½–1 mm thick, branched. Floating leaf 2–5 cm long by ½–2 cm wide, acute at base and tip, on a petiole ½–1 mm thick. Submersed leaf flaccid, 2–13 cm long ..... ***P. oakesianus***

18. a. Submersed leaves sessile **19**

b. Submersed leaves on petioles 0.5–4 cm long **21**

19. a. Floating leaves subsessile or very short-petioled. Submersed leaves 7- to 9-veined, tapering to base and apex. Plant commonly reddish-tinged ..... ***P. alpinus***

b. Floating leaves with petioles usually at least 2 cm long **20**

20. a. Submersed leaves lanceolate, usually less than 10 cm long, often crowded on densely branched lower stems, with midvein less than 1 mm wide ..... ***P. gramineus***

b. Submersed leaves linear, 10 cm or more long, on an unbranched or sparsely branched stem. Midvein conspicuous, 2 mm or more wide, including the adjacent bands of air channels (lacunae) ..... ***P. epihydrus***

21. a. Submersed leaves broadly elliptic, up to 5 cm wide, but commonly folded and falcate-recurved, entire-margined ..... ***P. amplifolius***

b. Submersed leaves not folded or falcate-recurved, with minute marginal teeth (difficult to see) **22**

22. a. Submersed leaves mucronate at tips, 2–5 cm wide, on petioles 0.5–2 cm long. Floating leaves (if present) on petioles usually shorter than blades. Transitional leaves often present ..... ***P. illinoensis***

b. Submersed leaves acuminate, 0.5–2 cm wide, on petioles usually over 2 cm long. Floating leaves on petioles at least as long as blades ..... ***P. nodosus***

Potamogeton alpinus Balbis — Alpine Pondweed

Generally reddish-tinged rhizomatous plant with unbranched or sparsely branched stems up to a metre or more long, but usually shorter.

Submersed leaves lanceolate to narrowly elliptic, tapering to a sessile base and acute to rounded apex, 7–20 cm long by about a tenth to a fifth as wide; usually 7-veined, thin and translucent; with broad, thin, free-margined ligular sheaths quite free of the leaf bases. Floating leaves (often absent) obovate, broader than the submersed ones, relatively thick and firm, and with more veins, the blades up to 6 cm long by 2.5 cm wide, tapering to short petioles. Transitional leaves often present, even when floating leaves absent.

Peduncle red, about as thick as the stem or slightly thicker. Spike with 5–9 whorls of flowers, up to 3.5 cm long at flowering time, elongating somewhat in fruit. Achene 3–4 mm long including the curved terminal stylar beak, with a sharp dorsal keel, orange to reddish when ripe.

KEY TO VARIETIES IN BRITISH COLUMBIA

1. a. Submersed leaves lanceolate, 8–10 times as long as wide, with obtuse to acute apices ..... var. ***tenuifolius***

b. Submersed leaves more elliptic, less than 8 times as long as wide, the apices rounded, sometimes slightly hooded ..... var. ***subellipticus***

Figure 24. *Potamogeton alpinus*: A, plant from shallow water; B, flower; C, achene.

P. alpinus is circumboreal in distribution. Variety *alpinus*, the typical form of the species, which is distinguished from our varieties by its achene with a straighter beak and more convex ventral margin, occurs from Europe to central Asia. Variety *tenuifolius* (Rafinesque) Ogden occurs from eastern Siberia across North America to Greenland, and variety *subellipticus* (Fernald) Ogden across North America. Generally northern and alpine or subalpine in range, *Potamogeton alpinus* is found as far south as Colorado and California at high altitudes. It grows in shallow, cold ponds and lakes, commonly where non-calcareous or with bottom deposits high in organic matter, in water from ½ to 1½ (exceptionally to 3½) metres deep (*see* map p. 139).

***Potamogeton amplifolius* Tuckerman** **Large-leafed Pondweed**

Coarse plant, 1 to 5 m or more long, with stems up to 3 mm thick, sparingly branched, from a long coarse rhizome.

Leaves of two kinds: submersed leaves on short petioles usually 1–2 cm long, the blades up to 20 cm long by up to 7.5 cm wide, typically folded along the midvein, and falcate-recurved as seen from the side, and loosely undulate, as the margins grow more than the midvein, with 19–45 longitudinal veins, olive green and translucent, deeper leaves narrower, fewer-veined, and straighter; floating leaves with petioles longer than the elliptic blades, which are relatively thick and opaque, green and flat, 5–10 cm long by 2–4 cm wide, with 25–45 longitudinal veins. Sheaths translucent, whitish, acute, with free margins, up to 10 cm long.

Peduncles enlarged upward. Spikes densely flowered with up to 16 whorls of flowers, and 1 cm or more thick in fruit. Achene obovoid, 4–5 mm long, with a stout beak 0.5-1 mm long, with a recurved stigma at the tip. Dried achenes show prominent dorsal and lateral keels, which are not visible on fresh achenes. Ripe achenes are orange to pinkish in colour.

This species ranges discontinuously across North America, and from southern British Columbia south to California in the west. It grows in deep clear water to 4 m deep, or rarely to 6 m in very clear water. It may show a high rate of spring growth; plants over 3 m long have been observed at the beginning of May in the Victoria area.

Some plants in Thetis Lake, near Victoria, combine the coarse stems and green floating leaves of *P. amplifolius* with the sharply 2-keeled sheaths and lowest leaves reduced to bladeless petioles of *P. natans*. The upper submersed leaves have long (to 12 cm) petioles, and long, narrow (to 12 × 1.5 cm), inrolled blades. The pollen grains are nearly all empty, and no mature fruit has been formed. This plant is believed to be the previously unrecorded putative hybrid: *P. amplifolius* × *natans*. Both the parent species occur nearby (*see* map p. 140).

***Potamogeton crispus* L.** **Crisped Pondweed**

Extensively growing, freely branching, leafy-stemmed plant with flat, wing-edged stems. Rhizomes are produced that may overwinter in mild conditions, but the usual method of overwintering vegetative propagation is by winter buds. Each such bud germinates in spring to produce several shoots and rhizomes from small buds in the axils of its reduced leaves.

Leaves alike and all submerged, oblong, up to 10 cm long by 1 cm wide, stiff and rather cartilaginous in texture, translucent, with 3 main veins, and notably dentate and undulate margins. Winter grown leaves may not have undulate margins. The first node on a branch produces a sheath without an associated leaf blade. Sheaths delicately membranous, free of the leaf bases, with overlapping margins, closely surrounding the stem, soon disintegrating.

Peduncles curved, somewhat dilated above, about twice as long as the 1–3 cm long spikes. Flowers with long-clawed tepals and carpels tapering into prominent stylar beaks. Achenes 4–6 mm long, including a beak 2–3 mm long, with a strongly toothed keel.

A species of European origin, commonly grown in aquaria and discarded into ditches, etc., it has become locally an aggressive weed in lakes and in deeper ditches and canals (*see* map p. 140).

***Potamogeton diversifolius* Rafinesque**

Freely branched plant up to ½ m long, with slender terete stem; propagating vegetatively by winter buds produced from upper leaf axils in autumn.

Leaves of two kinds. Submersed leaves sessile, linear, up to 4 cm long by 1½ mm wide, 1–3 veined, acute to obtuse at tips, adnate at base to the lower third of the stipular sheath. Floating leaves with elliptic blades up to 3 cm long, rounded at apex, on petioles about half as long which are free

Figure 25. *Potamogeton amplifolius*: A, upper part of plant with fertile shoot, and submerged sterile shoot; B, flower; C, achenes.

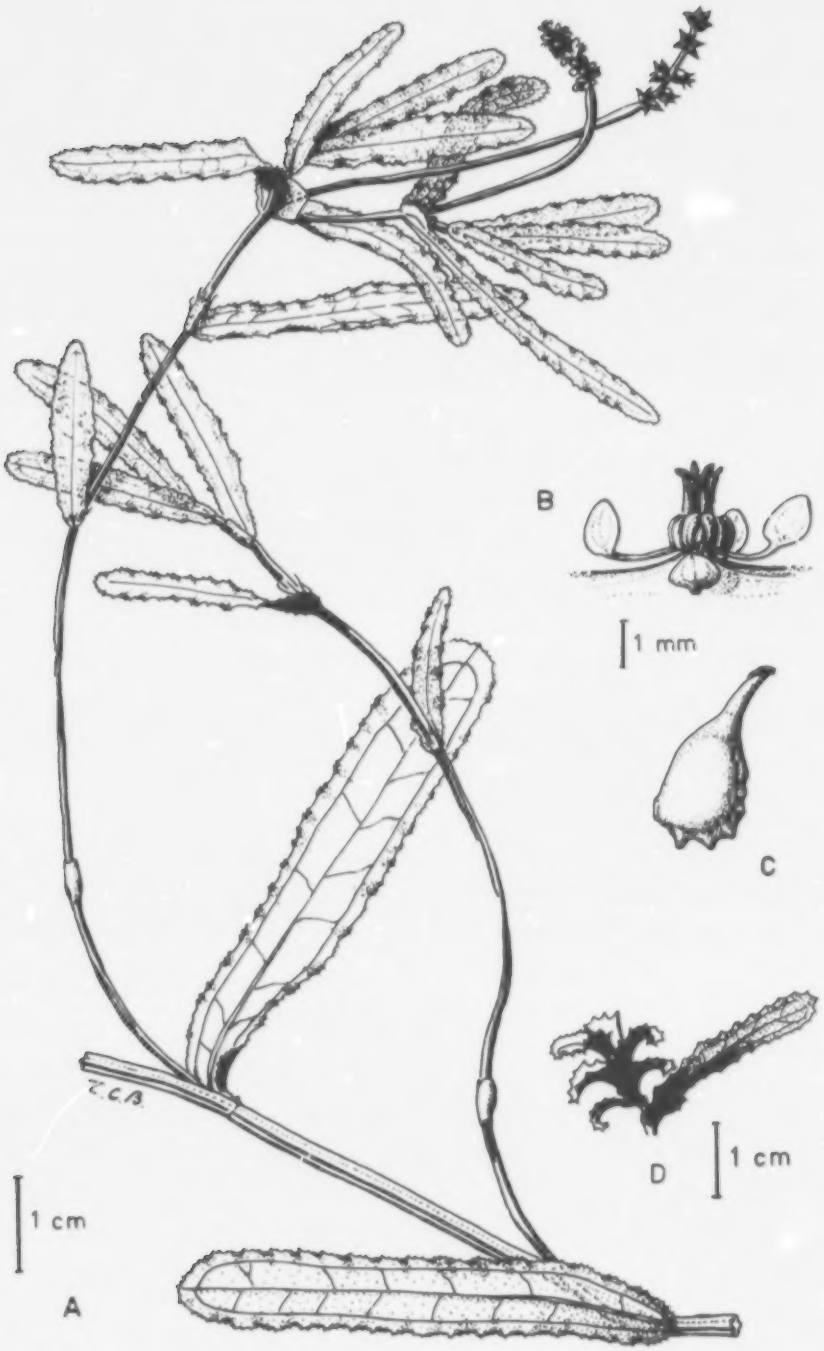


Figure 26. *Potamogeton crispus*: A, plant; B, flower; C, achene; D, winter bud.

Figure 27. *Potamogeton diversifolius*: A, plant; B, achene.

from or barely adnate to the sheaths. Sheaths up to 1 cm long at submersed leaves, up to 3 cm long at floating leaves; open to base on the side opposite the leaf base.

Peduncles and spikes very short, appearing beneath the water as well as above; the lower spikes with 1–3 whorls of flowers, the upper, emersed spikes with up to 6 whorls. Achene compressed, 1–1.8 mm long, distinctly keeled on the dorsal margin, with a very short straight beak. Embryo coiled into more than a complete turn, discernible externally.

A species of southern distribution, ranging across the United States, northward into Alberta, and southward into northern Mexico. In British Columbia, known so far only at Steelhead, near Mission, in the lower Fraser Valley (*see* map p. 141).

Potamogeton epihydrus Rafinesque

***P. epihydrus* var. *nuttallii* (Chamisso and Schlechtendal) Fernald = var. *ramosus* (Peck) House**

Rhizomatous perennial, the stem moderately compressed, creeping to erect, and sparingly branched or unbranched. Sometimes reproducing by large winter buds.

Leaves of two kinds. Submersed leaves linear and ribbon-like, 4–25 cm long by 2–10 mm wide, shortly tapering to cuneate sessile bases and acute tips, flaccid, with 3–13 longitudinal veins, the midvein bordered by conspicuous bands of loosely cellular lacunate tissue. Floating leaves with narrowly obovate to elliptic, leathery blades, 3–8 cm long by 1.5–3.5 cm wide, with up to 40 veins, rounded to obtuse at tips and tapering to cuneate bases, on petioles from shorter than to rather longer than the blades. Transitional leaves also occur. Submersed leaves and their sheaths on fertile shoots often decadent by flowering time. Sheaths delicately membranous, free of leaf bases, translucent, up to 4 cm long, obtuse on submersed leaf nodes, somewhat longer and attenuate on nodes bearing floating leaves.

Peduncles up to 16 cm long, as thick as stem or somewhat thicker, not tapering. Spike 2–4 cm long, with 7–12 whorls or pairs of flowers. Spikes may arise at nodes bearing submersed leaves, especially in deep clear water. Achene nearly circular, flattened, with a pronounced dorsal keel, in dried material at least, and the beak, if any, inconspicuous (*see* map p. 141).

KEY TO VARIETIES

1. **a.** Submersed leaves 5–10 mm wide, with 7–13 veins. Floating leaves broadly elliptic, up to 35 mm wide, with 20–40 veins ..... var. ***epihydrus***
   b. Submersed leaves 2–8 mm wide, with 3–7 veins. Floating leaves narrowly obovate to oblanceolate, 5–25 mm wide, with 7–33 veins ..... var. ***ramosus***

These varieties occupy much the same range generally, and intergrade completely. Most British Columbian material appears to be of var. *ramosus* (Peck) House [var. *nuttallii* (Chamisso and Schlechtendal) Fernald].

This transcontinental species ranges from Alaska to Labrador, and southward over all but the southernmost United States, with an outlying range in Scotland. It is found in shallow (½ m) to deep (3 m) clear water, often with a silty or sandy bottom.

Potamogeton filiformis Persoon

Entirely submersed perennial, over-wintering as small tubers terminating the slender buried rhizome. Stem filiform, terete, freely branched, sometimes with more than one branch at a node; the plant often having the aspect of a small dense brush.

Leaves filiform, up to 10 cm long by 0.5–1.5 mm wide, tapering to an acute tip, 1-veined, often brownish in colour. Stipular sheath membranous, adnate to the leaf base for most of its length, tubular below with connate margins, at least when young, though commonly ruptured and split to the base later by growth of an axillary branch.

Peduncle filiform, up to 15 cm long, bearing an open spike of 2–5 whorls of flowers, the lowest whorl often remote from the others. Achene obovoid, 2–3 mm long, beakless, with a sessile stigma, and no distinct keel on fresh material, though dried achenes may have keel-like wrinkles; light brown when ripe.

This species ranges over most of the Northern Hemisphere, extending south to Africa and Australia. It occurs in still or slow-moving, often calcareous water, commonly in shallower water (15–100 cm) than that inhabited by the related *P. pectinatus* (*see* map p. 142).

Figure 28. *Potamogeton epihydrus*: A, plant; B, achene.

Figure 29. *Potamogeton filiformis*: A, plant; B, rhizome with tubers; C, leaf base and stipular sheath; D, achene.

This species is said by Sculthorpe (1967) to be pollinated by floating non-wetting pollen. However, spikes bearing fruit have been seen among the foliage of this plant well below the water surface, suggesting that pollination may at times be effected by completely submerged pollen transferred between submerged flowers.

***Potamogeton foliosus* Rafinesque**

Submersed plant with filiform rhizomes. Stems up to 1 m long, freely and divergently branching, slender, slightly flattened, without paired glands at the nodes. Prerennation can occur by winter buds produced on the ends of short lateral branches or in leaf axils.

Leaves all alike, sessile, narrowly linear, 2–10 cm long by 1–2.5 mm wide, acute-tipped, with 1–5 veins, the midvein usually bordered by air channels at least near the base. Sheath free from the leaf base, with connate margins below when young, later ruptured by axillary branch growth, finally disintegrating.

Peduncles short, 1–3 cm long, the spike ½–1 cm long, with 2–4 whorls of flowers initially crowded but later separated by elongation of the axis. Sepals 0.4–1 mm long. Achene about 2 mm long, with a conspicuous undulate dorsal keel and a beak up to ½ mm long.

KEY TO VARIETIES

1. a. Leaves 1.5–2.5 mm wide, with 3–5 veins. Stems sparingly branched	var. ***foliosus***
b. Leaves 1.5 mm or less wide, with 1–3 veins. Stems freely branched	var. ***macellus***

This species is widespread in North and Central America. Variety *foliosus* is generally more southern, its occurrence in British Columbia being uncertain. Variety *macellus* Fernald is more northern in range, reaching the Northwest Territories, but overlapping with var. *foliosus* in the United States; is the common variety in British Columbia. Plants typically occur in marshes and shallow standing water (*see* map p. 142).

***Potamogeton friesii* Ruprecht**
***(? P. compressus* L.?)**
(P. mucronatus* Schrader *nomen nudum)

Submersed plants, sometimes with slender rhizomes, with freely branching, slender, flattened stems up to 1 m long, with paired yellowish translucent glands at the nodes. Perennating by winter buds of peculiar structure, which are borne on the ends of short axillary branchlets. These buds, which average about 2–2.5 cm long, bear two ranks of short stiff leaves, with their vascular strands stiffened with fibrous tissue at their bases. The stipular sheaths are divided fore and aft, and the resulting half-sheaths, white and fibrous, diverge in two ranks in a plane perpendicular to that containing the leaves.

Leaves all alike, sessile, linear, up to 8 cm long by 3 mm wide, rounded and mucronate at the tips, commonly with 3–5 veins. Sheaths conspicuous, up to 18 mm long, white, fibrous, and opaque, with margins connate when young; finally shredding into the persisting fibres.

Peduncles flattened, curved at base, up to 5 cm long, but commonly less. Spikes emergent at flowering time, 1–2 cm long, with 2–4 whorls of flowers. Achenes 2–2.5 mm long, with obscure rounded dorsal keel and a more or less curved terminal beak up to 0.6 mm long.

Widespread and circumboreal in the Northern Hemisphere; transcontinental in Canada, Alaska and northern United States. Found in fresh to brackish still water, ½–1½ (exceptionally to 3½) m deep (*see* map p. 143).

Specimens intermediate in character between this species and *P. zosteriformis*, having the slender, flattened but unwinged stem, not narrowed at the nodes, of *P. friesii*, with leaves 6–12 cm long by 1.5–3 mm wide having a few rather irregular interneural strands and acutish tips, stipules up to 3 cm long, and flowers with 1–3 carpels, but no mature fruit, have been found recently at Elk Lake, near Victoria, and at Lac la Hache. These plants are tentatively regarded as the previously unreported hybrid: *P. friesii* × *zosteriformis*.

Figure 30. *Potamogeton foliosus* var. *macellus*: A, plant; B, stipular sheath; C, achene.

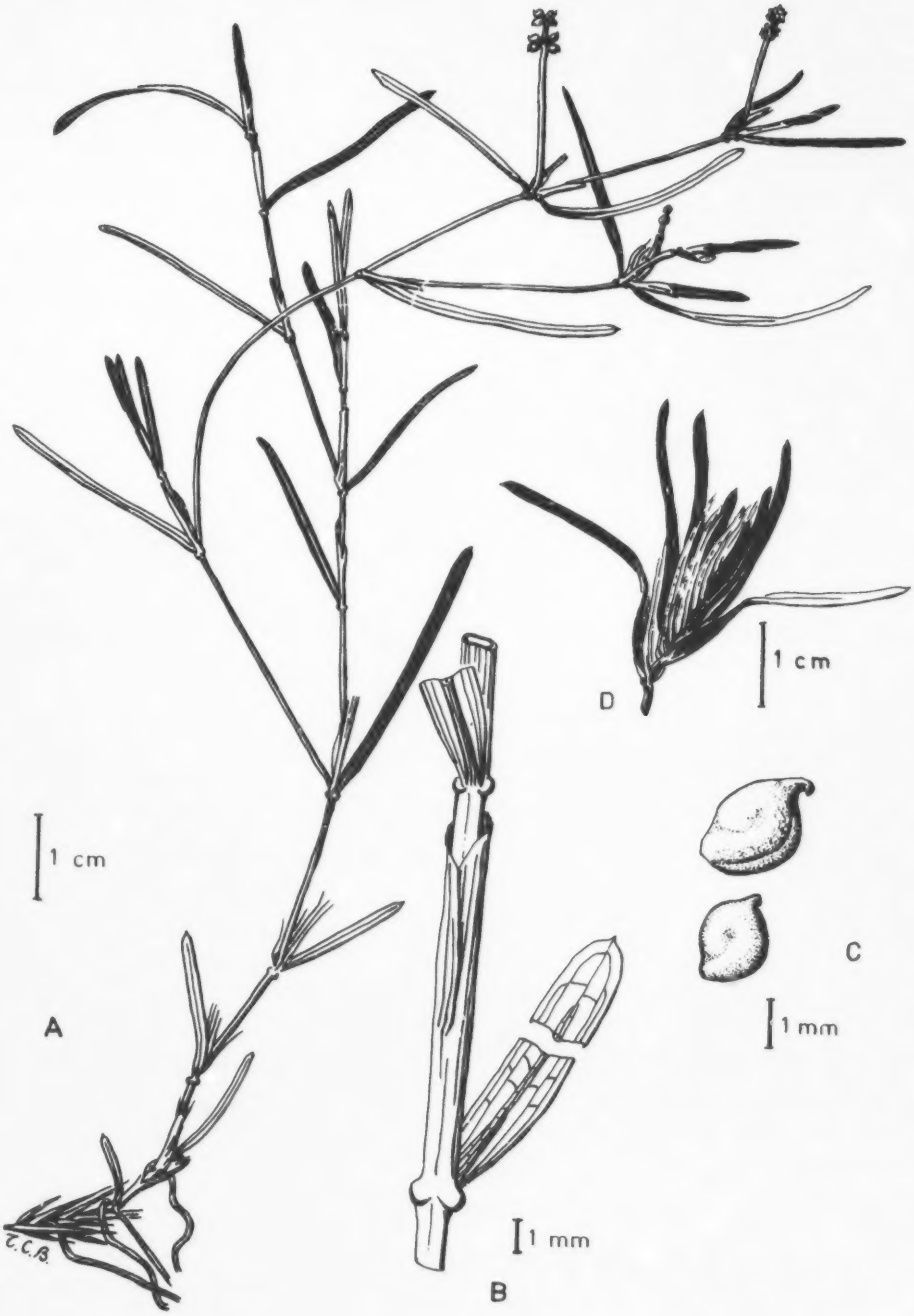


Figure 31. *Potamogeton friessii*: A, plant; B, detail of nodes, stipular sheath and leaf; C, achenes; D, winter bud.

***Potamogeton gramineus* L.**
(*P. heterophyllus* Schreber)

Our most variable species of this genus; a perennial with slender rhizomes that produce elongate tubers in autumn. Stems varying from a few centimetres to a metre or more long, according to situation, very slender, usually freely branched, occasionally with two branches in a leaf axil. Foliage bright green to bronzy or occasionally reddish.

Leaves of two kinds. Submersed leaves sessile, lanceolate to linear, diverse in size on one plant, those on lateral branches smaller than the main stem leaves, which may be up to 13 cm long by a centimetre or more wide, tapering to bases and to acute or acuminate tips, 3–11-veined, with a narrow midvein, and with minute one-celled marginal teeth that are barely visible at 10 × magnification. Floating leaves with elliptic blades up to 6 cm long by 1–3 cm wide, with up to 19 longitudinal veins, on petioles usually longer than the blades. Sheaths open down one side, up to 3 cm long.

Peduncles emergent, as thick as or thicker than the stems, and often thickened upward, of variable length up to 20 cm, according to situation. Spike dense, up to 3 cm long, with about 6 whorls or pairs of flowers. Achenes crowded, 2–3 mm long, rather flattened, with a dorsal keel and a short straight beak.

KEY TO VARIETIES

1. **a.** Submersed leaves on main axis lanceolate to narrowly elliptic, up to 13 cm long by 3–15 mm wide, 5–10 times as long as wide, with 5–11 veins 2
   b. Submersed leaves linear except for tapering ends, up to 6 cm long by 1–3 mm wide, 10–20 times as long as wide, with 1–3 veins ..... var. ***myriophyllus***

2. **a.** Submersed leaves on main axis 2–6.5 cm long by 3–8 mm wide, with 5–7 veins. Stems normally profusely branched ..... var. ***gramineus***
   b. Submersed leaves on main axis 3–13 cm long by 6–15 mm wide, with 7–11 veins. Stem sparingly branched ..... var. ***maximus***

Widespread in temperate and subarctic regions of the Northern Hemisphere, this is a common species all over British Columbia.

Highly adaptable to local conditions, this plant may grow in water up to 2 m deep, or only a few centimetres deep, or may even be found stranded on muddy shores by receding water, but nevertheless growing and reproducing. Its form reflects its habitat; submersed or floating, leaves may be absent. In the latter case, in deep water, the plant may be sparsely branched, and may flower at submersed nodes with alternate (as opposed to the usual subopposite) leaves. This environmentally conditioned variability in gross form, superimposed on the genetically determined variation indicated in the key, is further extended by the tendency of this species to form hybrids with other, related, species. The overall result is a mystifying profusion of forms, many of which, when sterile, may be difficult to identify, even to the species.

The extreme diversity of form of this species has led to the publication of many varieties. Parallel series of varieties appear to have been published by European and North American authors, sometimes with overlapping circumscriptions. The consequent confusion of names can only be sorted out by someone with access to both original European and North American collections and literature. The varieties used here are those accepted by North American authors for North American material, a treatment that admittedly is something less than completely satisfactory.

Variety *gramineus* is the common one throughout this province. Variety *maximus* Morong ex Bennett occurs sporadically in the southern and central interior, usually in deeper water than the other varieties. Var. *myriophyllus* Robbins (= var. *graminifolius* Fries according to Fernald, 1921) has so far been collected only at a few places on Vancouver Island (*see* map p. 143).

***Potamogeton illinoensis* Morong**

Rhizomatous, long-stemmed plants up to over 3 m long, with simple or branched stems.

Leaves of two kinds. Submersed leaves ample, rather shiny and translucent, on petioles 1–3 cm long, with blades to over 20 cm long by 5 cm wide, lanceolate with cuneate bases and mucronate apices, with 9–19 longitudinal veins and conspicuous cross-veins, producing a netted appearance; the margins serrulate with minute, deciduous, 1-celled teeth. Floating leaves, when present, on petioles shorter than the blades; the blades 6–12 cm long by 2–6 cm wide, thick and opaque, with 13–29 longitudinal veins. Transitional leaves commonly produced, similar in texture to typical

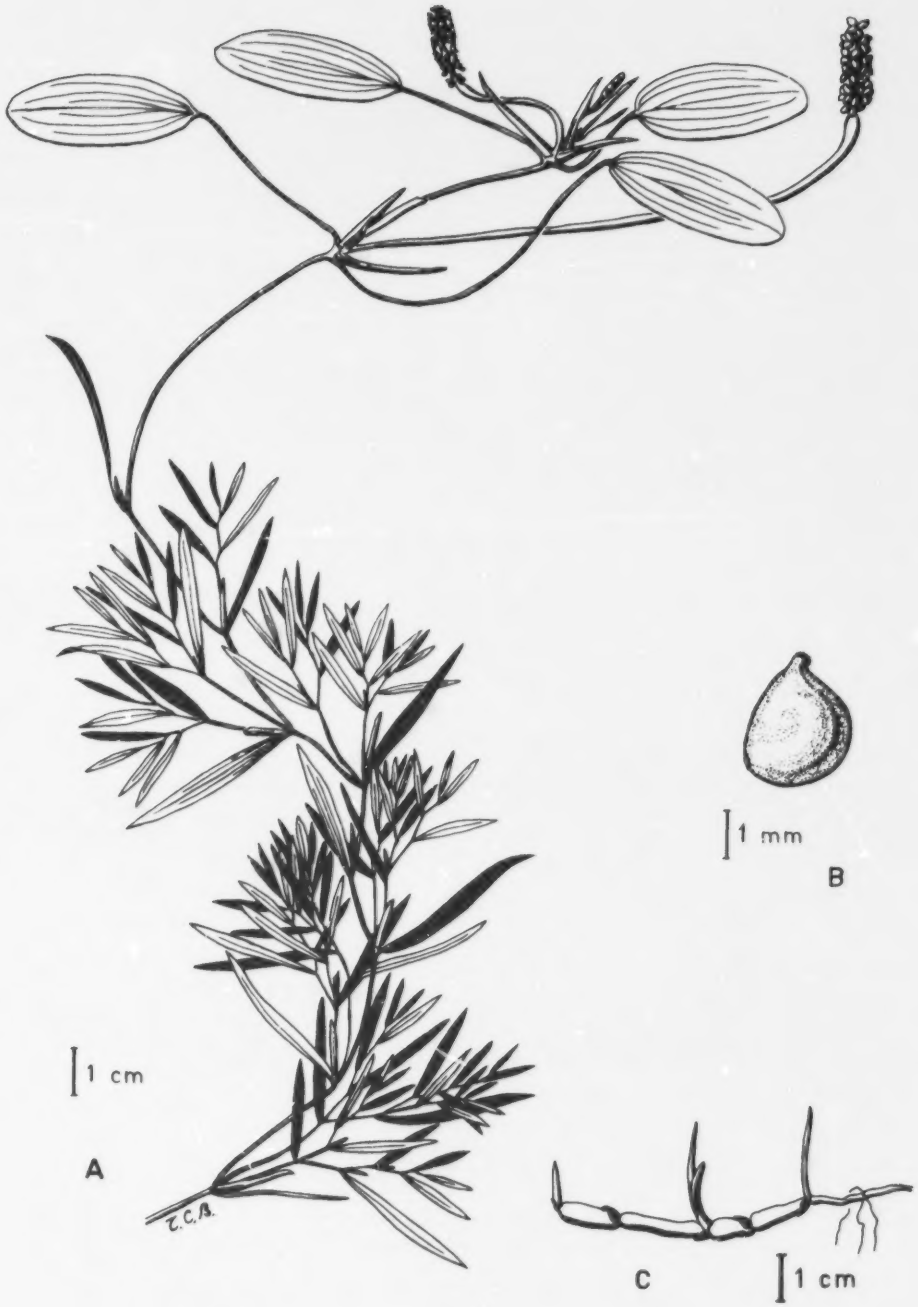


Figure 32. *Potamogeton gramineus*: A, plant of shallow water; B, achene; C, 2 tubers on rhizome.

Figure 33. *Potamogeton illinoensis*: A, fertile upper part of plant; B, achene; C, detail of leaf margin.

submersed leaves, but relatively shorter and broader, with rather longer petioles and more broadly rounded (but still mucronate) apices. Sheaths prominent, up to 10 cm long, open to base on one side, commonly with two dorsal ridges.

Peduncle thicker than the stem, commonly extending well beyond the foliage, and emergent. Flower spike at first compact, 3–6 cm long, later opening out somewhat, with around 15 irregular whorls of flowers. Achene about 4 mm long, including the 0.5 mm beak, with a prominent dorsal keel and sometimes lateral keels.

Widespread in the United States (except the southeast) and southern Canada. Found in deep still water of lakes or slow rivers, in water to 3 m or more deep (*see* map p. 144).

***Potamogeton natans* L.**

Rhizomatous perennial with strong, terete, green to brownish, usually unbranched stems up to 3 m long and 2 mm thick, but usually much shorter, and thinner, the rhizome commonly producing overwintering tubers.

Leaves of two kinds. Submersed leaves resembling stiff bladeless petioles, up to 50 cm long and 1–2 mm wide. Floating leaves (rarely absent) with petioles notably longer than the blades; their blades broadly elliptic, with commonly subcordate (occasionally cuneate or rounded) bases and rounded tips, up to 10 cm long by 6 cm wide, with 19–35 veins, coppery brown in colour in life. Transitional leaves, with very small blades, are sometimes found in spring. Sheath free of petiole base, stout, 2-keeled, stiff, and fibrous, up to 18 cm long, ultimately shredding into fibres.

Peduncles up to 12 cm long, emergent, thicker than the stem. Spike up to 3 cm long, compact and densely flowered. Achene obovoid, 3–5 mm long, including a straight apical beak 0.5–1 mm long, khaki-brown when ripe, keeled or rounded dorsally when dry, the keel not conspicuous on fresh material.

Widespread in temperate latitudes of the Northern Hemisphere; one of our commoner species of this genus. Found in shallow to moderately deep (1–3 m) waters of sheltered bays and ponds, often where the bottom incorporates organic matter. Under some conditions, winter buds may be produced from the upper leaf axils on the stem. These buds bear leaves like abbreviated forms of the submersed leaves. In mild areas, the entire shoot may survive over winter (*see* map p. 144).

***Potamogeton nodosus* Poiret**

Rhizomatous perennial with terete, unbranched or sparingly branched stems up to 2 m long.

Leaves of two kinds, all petioled. Submersed leaves on petioles 2–10 cm long, with blades lanceolate to narrowly elliptic, 10–30 cm long by 1–3 cm wide, acuminate, with 7–15 longitudinal veins, thin and translucent. Floating leaves leathery, with blades elliptic, 5–12 cm long by 1.5–4 cm wide, on petioles longer than the blades. Sheaths 3–8 cm long, free of the petiole, and open to base on one side.

Peduncles thicker than the stems, up to 15 cm long. Spikes up to 6 cm long, densely flowered with up to 15 whorls of flowers. Achenes obovoid, obscurely keeled when fresh, but prominently keeled when dry, almost beakless, or with a very short beak less than 0.5 mm long.

Very widespread, mainly in warmer latitudes, in North and South America, Eurasia and Africa. Not common in British Columbia. Growing in shallow to deep clear fresh waters of lakes and ponds (*see* map p. 145).

***Potamogeton oakesianus* Robbins**

Like a small, delicate, more branched version of *P. natans*. Stem 0.5–1 mm thick, ½–1 m long, with a branching pattern suggestive of *P. gramineus* var. *myriophyllus*.

Submersed leaves linear, the upper ones slightly dilated toward their apices, flat, thin, flaccid, 3–13 cm long by ½–2 mm wide, with 1–3 veins.

Floating leaf blades elliptic, acute at bases and apices, 7–25-veined, on long thread-like petioles. Stipular sheaths membranous to somewhat fibrous, greenish and opaque, tending to become detached at bases.

Spikes with 3–8 whorls of flowers, up to 3.5 cm long by 7–9 mm thick in fruit. Achenes 2.5–3.7 mm long, with a prominent dorsal keel.

A plant of eastern North America, this species has been found by A. and O. Ceska in a pond at Steelhead, in the lower Fraser Valley, probably as an introduction. Material seen to date has been sterile (*see* map p. 145).

Figure 34. *Potamogeton natans*: A, flowering shoot; B, achene (dried).

Figure 35. *Potamogeton nodosus*: A, fruiting shoot; B, achene.

Figure 36. *Potamogeton oakesianus*: Sterile shoot.

Potamogeton obtusifolius Mertens and Koch

Submersed plants ½–1 m long, green or reddish, with terete or somewhat flattened, slightly zigzag stems bearing paired swollen glands at the nodes. Perennating by densely leafy winter buds, that terminate vegetative branches in fall, and lie on the bottom of the water over winter to sprout in spring.

Leaves all alike, sessile, broadly linear, up to 10 cm long by 4 mm wide, rounded to sometimes acute at tips, translucent, green or reddish, with usually 3 veins, rarely more, the midvein bordered by 2–4 rows of air channels. Sheaths about 2 cm long, open to base on the side opposite the leaf base, sometimes rather flaring, eventually shredding into fibres from the tips.

Peduncle straight, short, up to 2 cm long. Spike short, 1–2 cm long, densely flowered. Achene 3–4 mm long, rounded or obscurely keeled dorsally, with a straight beak up to 0.7 mm long.

Widespread in the Northern Hemisphere but scattered and uncommon in British Columbia. In shallow lakes and ponds, often with bottoms of organic sediment (*see* map p. 146).

Potamogeton pectinatus L. — Sago Pondweed

Entirely submersed plant with several stems ascending from a buried, extensively branched, slender rhizome, that produces small over-wintering tubers. Stems terete, filiform, frequently branching, with one, or sometimes two, branches in a leaf axil, the branches often having a tuft-like or fan-like appearance.

Leaves all alike, filiform, 2–12 cm long by up to 1 mm wide, tapering to an acute tip, usually with 1 vein, rarely with 3. Stipular sheath membranous, adnate for most of its length to the leaf base, 2–3 cm long, the margins overlapping, but separate to the base on the side opposite the leaf.

Peduncle filiform, lax, not raising the flower spike above the water, the spike usually lying horizontally at or just beneath the surface. Spike 1–3 cm long at flowering time, of 2–5 whorls of flowers, the lowest often remote from the others; the axis elongating in fruit. Achene 3–4.5 mm long, with a beak up to 0.7 mm long, reddish-brown when ripe.

Widespread in the Northern Hemisphere; common all over British Columbia. Inhabiting still or slowly moving fresh water from ½ to 2½ m deep, this species can tolerate a moderate degree of salinity or alkalinity, and is found in brackish marshes and very calcareous waters (*see* map p. 146).

Potamogeton perfoliatus L.

***P. perfoliatus* var. *richardsonii* Bennett, *P. richardsonii* (Bennett) Rydberg = *P. perfoliatus* ssp. *richardsonii* (Bennett) Hulten**

Sparsely branched, immersed plant with long cylindrical stems bearing leaves at frequent and regular intervals and spreading by buried creeping rhizomes.

Leaves all submersed and alike, sessile, broadly ovate to lanceolate, 2–13 cm long by 1–3 cm wide, clasping the stem at their cordate bases, with 7 to many longitudinal veins and fine cross-veins, the margins with minute one-celled teeth. Sheaths variably membranous with few to many incorporated fibres, tending to disintegrate early.

Peduncles commonly short and stout, moderately dilated above, often becoming recurved; commonly but little longer than the spike, but sometimes very elongated. Spike short, dense, of 4–12 whorls of flowers, 2–4 cm long, becoming 1 cm thick in fruit. Achene 2.5–4 cm long, including the 0.5–1 mm long beak. Usually without a keel.

KEY TO SUBSPECIES

1. **a.** Stem and peduncle relatively slender. Leaves broadly ovate, rounded at apex, often straight, occasionally recurved. Sheath membranous, with few short fibres, soon disappearing ..... ssp. ***perfoliatus***
   b. Stem stouter. Peduncle thickened distally. Leaves more narrowly ovate to sublanceolate, acute at apex, often recurved and with undulate margins. Sheath with many strong white fibres that persist as the membranous parts decay ..... ssp. ***richardsonii***

Subspecies *perfoliatus*, the common subspecies across Eurasia, is also found along the Atlantic coast of this continent, and in Alaska, Yukon, and extreme northern British Columbia. In this province, it is known only from Swan Lake, in the Cassiar Range, up till now.

Subspecies *richardsonii* (Bennett) Hulten [*P. richardsonii* (Bennett) Rydberg], the common subspecies in North America, is abundant throughout this province (*see* map p. 147).

These subspecies are often maintained as separate species. However, since the character distinctions are not as clear-cut as the published descriptions would suggest, and as intermediate or

Figure 37. *Potamogeton obtusifolius*: A, fruiting shoot; B, achene.

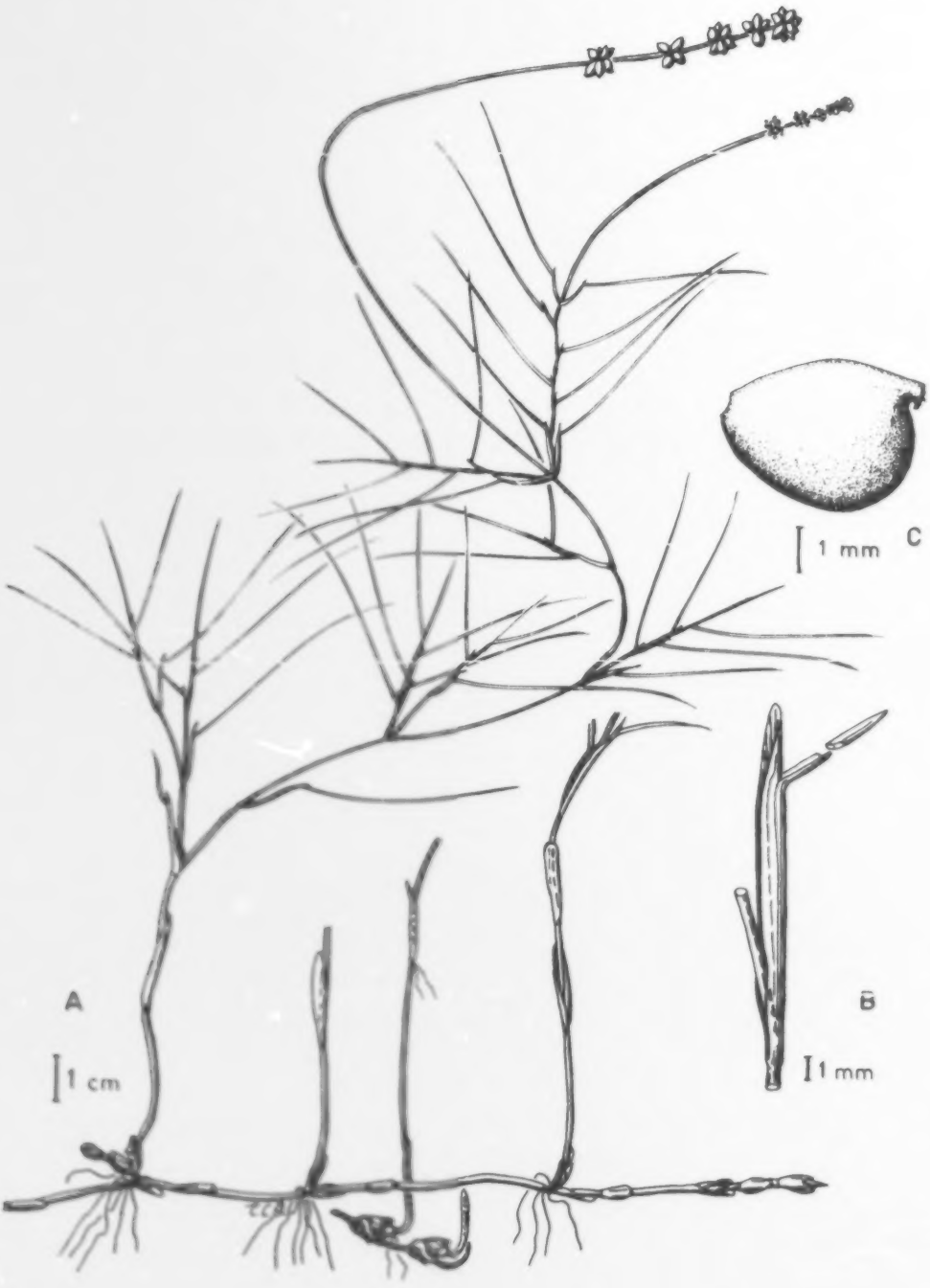


Figure 38. *Potamogeton pectinatus*: A, shallow-water plant, flowering and fruiting, and tubers; B, stipular sheath and leaf base; C, achene.

Figure 39. *Potamogeton perfoliatus* ssp. *perfoliatus*: A, shallow-water plants; B, flower; C, achene.

Figure 40. *Potamogeton perfoliatus* ssp. *richardsonii*: A, upper plant, flowering and fruiting; B, flower; C, achene.

indeterminate specimens are found in widely scattered localities, it is thought better here to include them both in one species. The sheath characters are the most reliable for distinguishing between these subspecies, but even these can be misleading sometimes, when not taken in conjunction with other characters.

Potamogeton perfoliatus is widespread in the Northern Hemisphere, and is probably our most abundant species of this genus. It is found in shallow to deep clear lake waters, ½–3½ m deep, often where slightly alkaline, or in slow-flowing rivers. This species shows much variation among individuals in such characters as the spacing, size and form of the leaves, and the length of the peduncle. This variation is little understood, but the basis appears to be partly genetic, and partly a response to conditions such as the depth of water and the advance of the season's growth (Spence and Dale, 1978).

***Potamogeton praelongus* Wulfen**

The largest of our pondweeds. Immersed rhizomatous perennial with a stout, brown-spotted white rhizome 2–6 mm thick containing numerous air passages. Erect stems 2–6 m long and 2–3 mm thick, with stout, shiny, often zigzag upper stems producing frequent branches toward the top, though sparingly branched below.

Leaves all alike in general form, sessile, shiny, 7–30 cm long by 15–25 mm wide, commonly clasping the stem by their cordate or subcordate bases, widest below the middle, whence tapering gradually to rounded, rather hooded tips, with 5 or more stout longitudinal veins with finer intermediate veins and cross-veins. Leaves on the short axillary branches are generally smaller than those on the upper main stem, and deeper leaves are generally shorter, and less cordate, or even cuneate at bases. Sheaths free from leaf bases, stiff, whitish, 3–10 cm long, persistent or eventually disintegrating.

Peduncles emergent, stout, 1–5 dm long, somewhat thickened upward. Spikes up to 5 cm long with 6–12 close-set whorls of flowers. Achenes 4–8 mm long, including the very stout 0.5–1 mm beak, distinctly keeled dorsally.

Circumboreal in distribution, south in North America into much of the United States. Typically found in deep clear lakes, it may grow in water up to 6 m deep. It is capable of a phenomenal rate of growth in spring; shoots having been found up to 5 m long by the beginning of May in the Victoria area. Late in the growing season, large winter buds may be formed in the upper leaf axils, for vegetative perennation. These winter buds are abbreviated branches, with short internodes, and crowded, diverging, short leaves emerging from beneath conspicuous white stipular sheaths (*see* map p. 147).

***Potamogeton pusillus* L.**

***P. panormitanus* Bivona-Bernardi**

***P. berchtoldii* Fieber, including var. *tenuissimus* (Mertens and Koch) Fernald and var. *lacunatus* (Hagstroem) Fernald = *P. pusillus* L. var. *tenuissimus* Mertens and Koch**

Fine-structured, usually profusely branched, submersed plant, up to a metre long, with slender, terete stems and often widely diverging branches, normally, but not invariably, bearing pairs of yellowish glands at the nodes. Commonly non-rhizomatous, and perennating by small winter buds (turions) formed in the leaf axils or on the ends of lateral branches late in the growing season.

Leaves all alike, submersed, sessile, linear, 2–7 cm long by 0.5–2 mm wide, normally 3-veined, acute to obtuse or rounded at the tips. Sheaths free from leaf bases, delicate, membranous rather than fibrous, translucent pale greenish, usually shed or disintegrating long before the leaves do; commonly 1 cm or less, but occasionally up to 3 cm, long.

Peduncles slender, 2–3, or sometimes to 5 cm, long, often strongly curved near base. Spike 3–15 mm long, with 1–4 whorls of flowers, usually, but not always, raised above the water surface briefly at flowering time. Achenes 1.5–3 mm long, rounded and keel-less dorsally, with a short beak up to 0.5 mm long; ripening under water.

KEY TO VARIETIES

1. **a.** Leaf with no air chambers (lacunae) or at most only one row on either side of the midvein. Sheath margins connate when young, later ruptured by growth of the axillary branch. Spike up to 15 mm long, of 2–4 whorls of flowers. Fruit widest above the middle ..... var. ***pusillus***

   b. Leaf with 1–5 rows of lacunae each side of the midvein. Sheath margins overlapping but free from the first. Spikes up to 7.5 mm long, with 1–3 whorls of flowers. Fruit widest at or below the middle ..... var. ***tenuissimus***

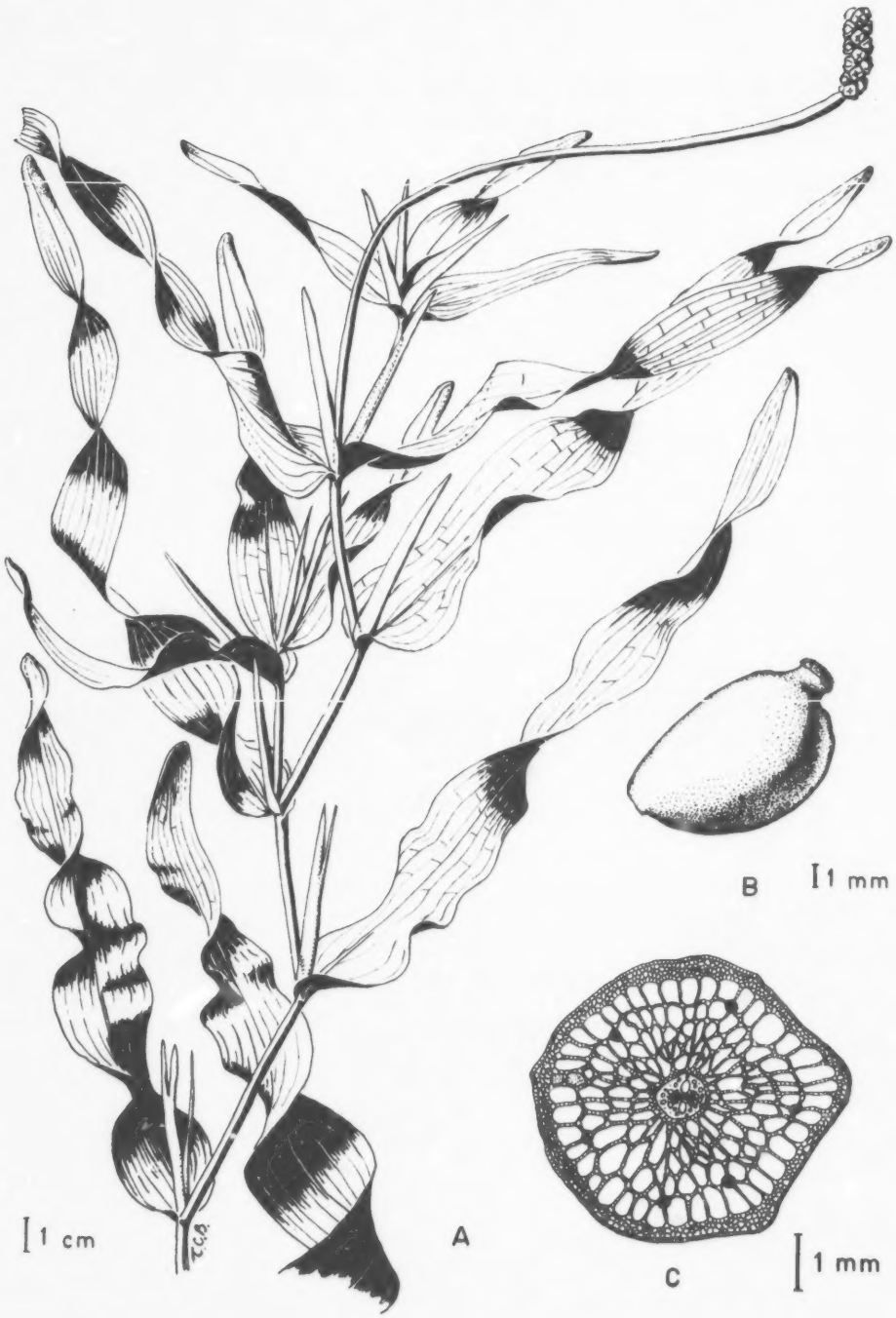


Figure 41. *Potamogeton praelongus*: A, upper plant; B, achene; C, cross-section of rhizome, showing spongy cortex (lacunate tissue) traversed by air passages separated by thin partitions, and the slender central vascular strand.

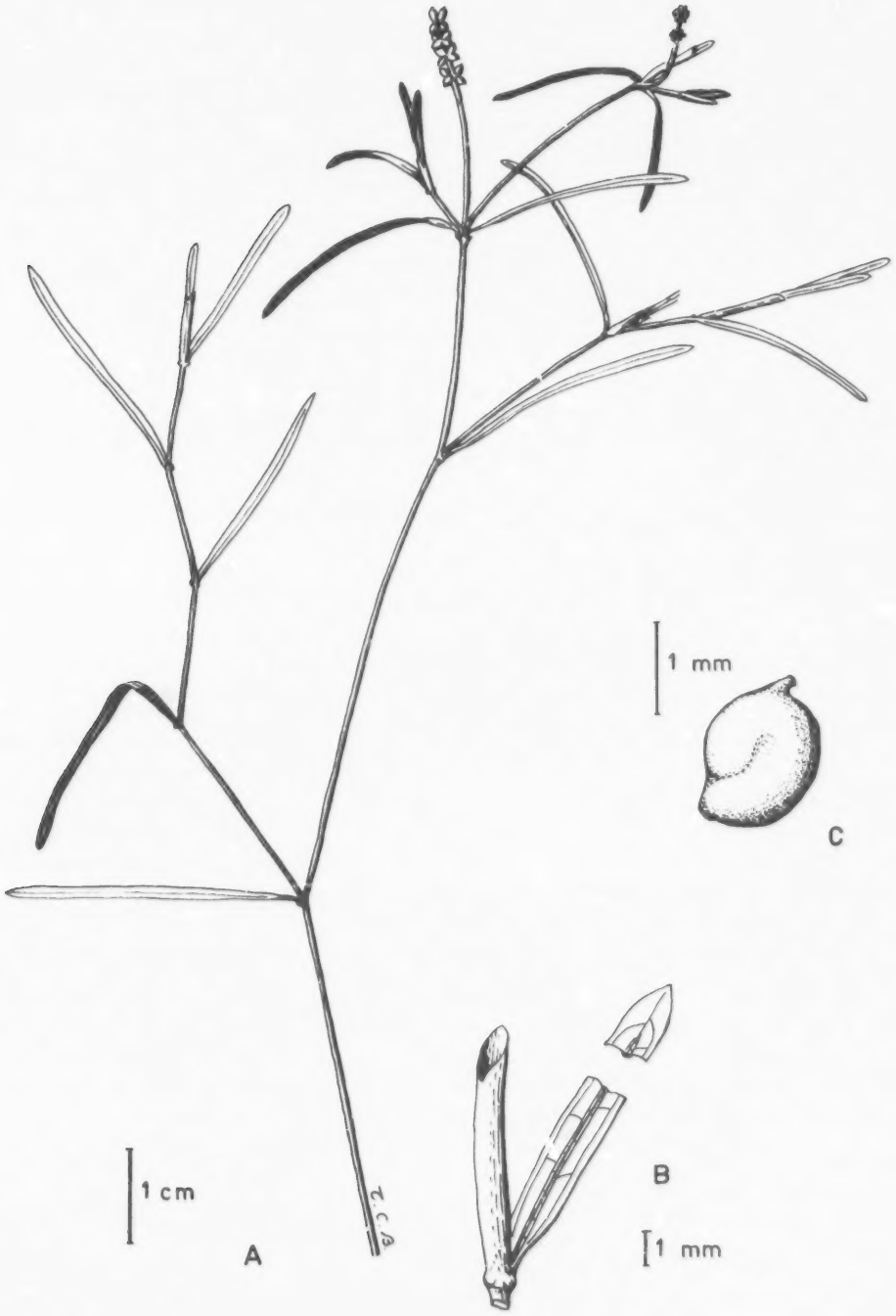


Figure 42. *Potamogeton pusillus* var. *pusillus*: A, fertile branch; B, detail of node ... sheath and leaf; C, achene.

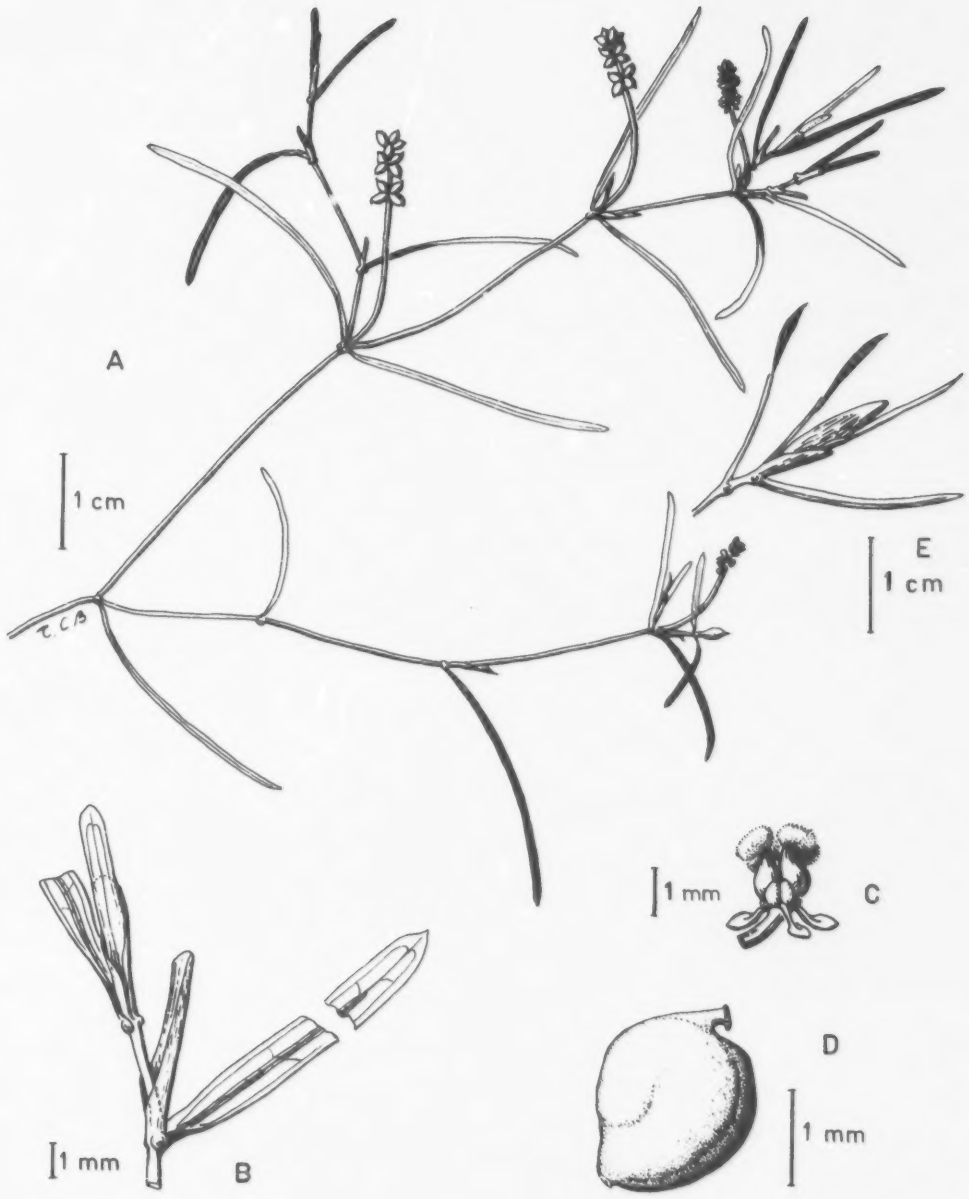


Figure 43. *Potamogeton pusillus* var. *tenuissimus*: A, fertile branch; B, detail of young shoot tip, nodal glands, stipular sheath and leaf; C, flower; D, achene; E, winter bud.

Distinction between these two entities, either as varieties or as species, has long been a source of confusion. No single character is 100% reliable in separating them: a consensus is preferable. The sheath character is commonly treated as decisive, but does not correlate perfectly with other characters. Care must be used in handling the sheaths, which are easily and soon split; and only the youngest ones should be used. Haynes' (1974) treatment of this complex, in uniting *P. berchtoldii* Fieber [including its var. *tenuissimus* (Mertens and Koch) Fernald and var. *lacunatus* (Hagstroem) Fernald] with *P. pusillus* as var. *tenuissimus* Mertens and Koch, is regarded as the most realistic, and is followed here.

This species is widespread in the Northern Hemisphere, and ranges all over North America. It is typically found in shallow fresh ponds and small lakes in water up to a metre deep, often in rather acid water. Leaves, while alike in form, may vary widely in size with the season, even on the same plant, and may also vary with variation in the habitat (*see* maps p. 148).

***Potamogeton robbinsii* Oakes**

Stem creeping on the bottom of the water, rooting at the lower nodes, moderately compressed, ½–3 m long. Leafy shoots prostrate and creeping, flowering shoots ascending toward the water surface.

Leaves crowded in one plane and obviously 2-ranked, stiff and widely diverging from the stem, linear-lanceolate, up to 12 cm long by 6 mm wide, dark olive to brownish green, and often covered by colonies of diatoms and other algae, with many parallel veins and white, finely serrulate margins, the subcordate base of the blade arising from about the mid point on the adnate stipular sheath. Stipular sheath 10–15 mm long, white, fibrous, shredding from the tip into its constituent fibres; commonly covering the stem between the leaves.

Flowering shoots ascending to near the water surface, with long internodes and shorter leaves than on vegetative shoots, branching and producing several flower spikes on flat stiff slender peduncles, each spike with about 4 whorls of flowers. Flowering late (July-September). Mature achenes 3–4 mm long, blackish, with a distinct dorsal keel and a curved beak up to 1 mm long. Mature achenes are very seldom produced and reproduction is generally vegetative by overwintering shoot-tips or, adjacent, coarse winter buds.

Widespread across Canada and northern United States, though not continuous. Found in shallow to deep (1–3 m) clear still water of sheltered bays or ponds, commonly with a bottom of muck or coarse vegetation detritus (*see* map p. 149).

***Potamogeton strictifolius* Bennett**

Somewhat resembling *P. friesii*, but rather sparingly branched, with relatively short internodes and crowded foliage. Stems somewhat flattened, but rather less so than in *P. friesii*, with paired glands at the nodes.

Leaves all alike, linear, 3–5 cm long by ½–2½ mm wide, stiff, acute at apices, with 3, or occasionally 5, longitudinal veins and few or no cross-veins, olive green to brownish. Midvein prominent, not bordered by lacunae or by one inconspicuous row each side. Margins often rolled under, appearing thickened. Stipules white, very fibrous, with connate margins below when young but becoming frayed into fibres with age, 1–2 cm long, often longer than the internodes and largely concealing the stem.

Peduncle filiform, thickened above, 1–9 cm long. Spike 1–1½ cm long, open, with 3–4 whorls or pairs of flowers. Achene 2–3 mm long.

Reproducing vegetatively by slender winter buds terminating sterile branches, and covered by appressed stipular sheaths and corrugated-based short blunt leaves.

Known from Saskatchewan to the northeastern United States, this species has been found in lakes at Hope and in Windermere and Columbia Lakes, in British Columbia (Ceska and Ceska, 1980). Fruit has not been found in British Columbia (*see* map p. 149).

***Potamogeton vaginatus* Turczaninow**

Completely immersed rhizomatous perennial, resembling *P. pectinatus*, but generally coarser, the stem terete, stout below but more slender above, freely branching, the main stem commonly giving off 2, and sometimes 3 or more branches at a node.

Leaves all alike, sessile, adnate to the stipular sheaths, linear, up to 10 cm or more long by 1–2 mm wide, rather thick, with 1–3 veins, and obtuse to rounded tips, often dark brownish in colour.

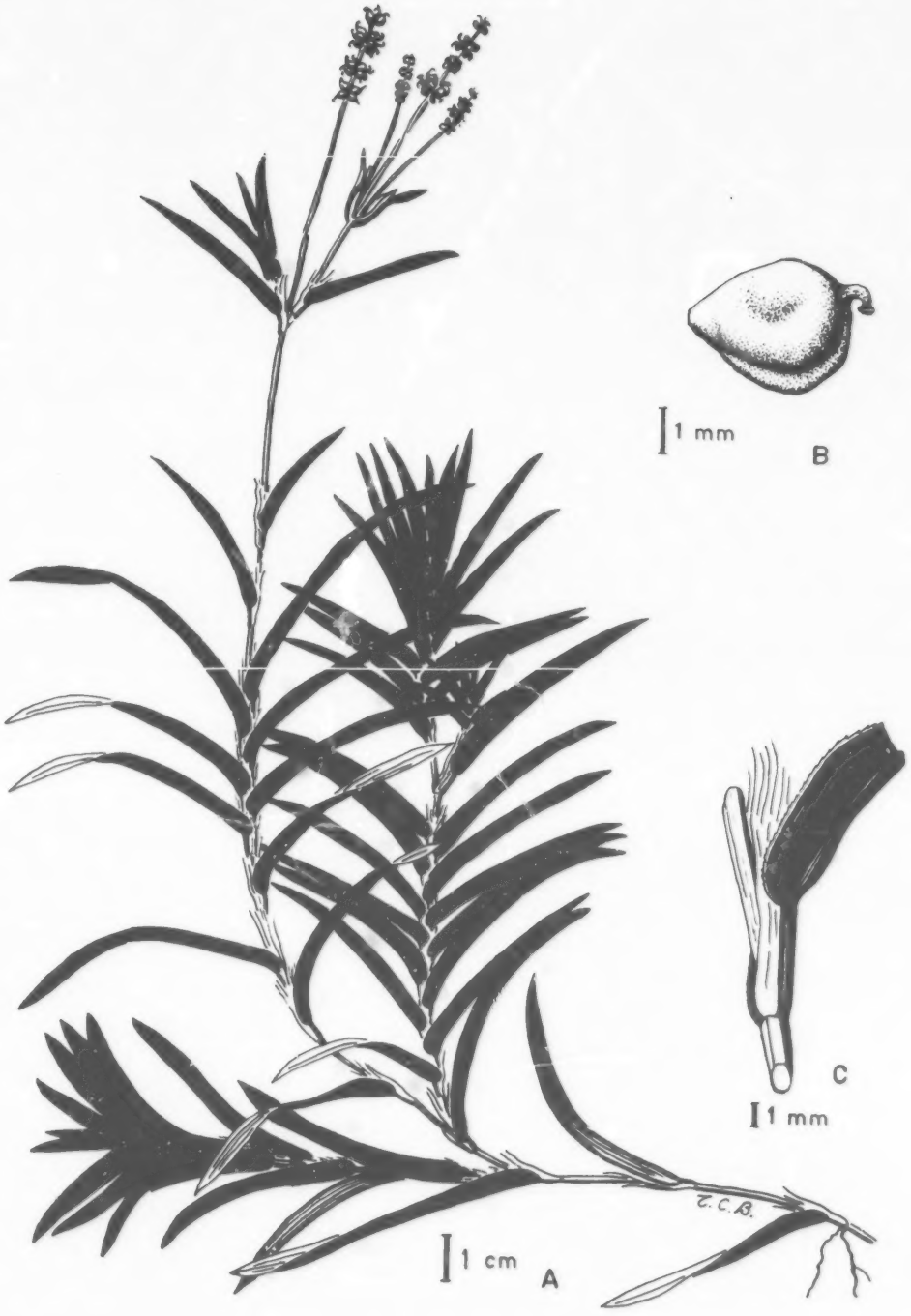


Figure 44. *Potamogeton robbinsii*: A, shallow-water plant; B, achene; C, stipular sheath and leaf base.

Figure 45. *Potamogeton strictifolius*: Plant with flowering shoot, and sterile shoots terminating in winter buds.

Figure 46. *Potamogeton vaginatus*: A, shallow-water fruiting plant; B, achene.

Stipular sheaths adnate for most of their length to the leaf bases, distended, conspicuous on the main stem where they may enclose the bases of multiple axillary branches, firm textured, the margins not connate.

Peduncle up to 12 cm long, slender. Spike elongate, with 5–9 evenly spaced whorls of flowers. Achenes obovoid, 3–4 mm long, obscurely keeled or rounded dorsally, and beakless, the stigma sessile.

Circumboreal in distribution, but rather scattered and less commonly seen than the related *P. pectinatus* in British Columbia. It inhabits cold lakes and slow rivers, especially where the waters are somewhat calcareous, in water 1½–3 m deep, generally deeper than that in which *P. pectinatus* is found (*see* map p. 150).

***Potamogeton zosteriformis* Fernald**

***P. zosterifolius* Schumacher ssp. *zosteriformis* (Fernald) Hulten**

Not *P. compressus* L. (*P. zosterifolius* Schumacher) *sensu* Dandy, 1980

Immersed perennial, sometimes rhizomatous, with flat, wing-edged, freely branched, zigzag stems up to 2 m or more long, and 2–3 mm wide, but constricted somewhat at the nodes, and sometimes with paired small greenish nodal glands. Perennating by winter buds 4–7 cm long.

Leaves all alike, sessile, linear, up to 20 cm long by 3–5 mm wide, scarcely narrowed at bases, rounded and mucronate at tips, rather stiff and straight, with 5 longitudinal veins, scattered cross-veins, and numerous fine longitudinal vein-like interneural strands of sclerenchyma with free ends. Sheaths free of leaf-bases, open to base on one side, firm and fibrous, white, eventually shredding into fibres.

Peduncle flattened, up to 10 cm long. Spike 2–2.5 cm long, closely flowered. Flower with only one carpel: one of the upper two. Fresh achene angularly broadly elliptic to suborbicular, 4–6 mm long, with a pronounced undulate and irregularly crested dorsal keel, and a stout, slightly curved stylar beak 0.6–1 mm long. Lateral keel-like wrinkles may appear on dried achenes.

Transcontinental in North America; widespread in Canada and in the northern United States. Not uncommon in lakes in the interior of British Columbia, in water 1–2½ m deep.

The closely related *P. zosterifolius* (= *P. compressus* L. according to many authors, including Dandy, 1980) of Eurasia differs in having, on the average, more slender stems, less constricted at the nodes, more fibrous stipules, and rather smaller, more narrowly elliptic achenes 2–4.5 mm long, and two carpels per flower (Dandy, 1980). The coarse extreme of Eurasian material identified as *P. compressus* seen by the author in this country closely resembles the average of North American material of *P. zosteriformis* in vegetative character (*see* map p. 150).

The Genus *RUPPIA* L.

Ditch-grass

Rhizomatous and stoloniferous perennials with slender filiform leaves and adnate stipular sheaths the ligules usually very short. Sterile plants strongly suggesting *Potamogeton pectinatus*.

Leaves of vegetative shoots alternate and 2-ranked, becoming subopposite at fertile branch-ends, with one vein per leaf.

Inflorescence a terminal pedunculate spike with two alternate flowers near the tip. Each flower has two very minute tepals which are adnate to the divided ends of the very short filaments of the two (upper and lower) stamens. Each stamen has two curved, extrorse, 2-chambered anthers that together encircle the axis of the spike. Between the stamens are normally four distinct unilocular carpels on initially very short stipes, with sessile stigmas and single pendulous ovules. Pollination generally at the water surface, with floating pollen.

Fruit a small achene (or barely fleshy and drupe-like), asymmetric or more or less symmetric, on the end of the elongate stipe. The peduncle may elongate considerably during anthesis or between then and the time of fruit maturation. The stipes also elongate as the fruits mature, so that the mature carpels of each flower attain an umbel-like arrangement.

Plants of saline, brackish or alkaline waters of marshes and lagoons along the coast and in lakes in the drier parts of the interior. Cosmopolitan.

Our material is confusingly diverse, varying in the expressions of several characters in ways that show little or no correlation. About 25 species have been described, those in this country at least being mixed with many intergradient forms. In the absence of really clear-cut distinctions among the various forms, it is felt that the best treatment here is to maintain all of them as varieties of one species under the oldest specific name.

Figure 47. *Potamogeton zosteriformis*: A, base and top of fruiting plant showing germinated winter bud at base; B, flower; C, achenes; D, leaf tip showing free-ending interneural strands.

***Ruppia maritima* L.** **Ditch-grass**

R. maritima* var. *rostrata* Agardh = var. *maritima

***R. spiralis* L. *ex* Dumortier; *R. maritima* ssp. *spiralis* (L. *ex* Dumortier) Ascherson and Graebner; = *R. maritima* var. *spiralis* (L. *ex* Dumortier) Moris**

R. cirrhosa* (Petagna) Grande = *R. maritima* var. *spiralis

***R. occidentalis* Watson = *R. maritima* var. *occidentalis* (Watson) Graebner**

Characters of the genus: varieties can be distinguished according to the following key, though some individuals do not conform to any one variety.

KEY TO VARIETIES

1. **a.** Stipular sheaths, at least some, on main stems, 2 to 7 cm long. Leaves 8 to 30 cm long, stiffish, often in conspicuous fan-like sprays. Peduncles long and helically coiled. Achene ± symmetric. Coarse stiff plants of interior lakes ..... var. ***occidentalis***
   b. Stipular sheaths all less than 2 cm long. Leaves up to 7 cm long. Fine-textured, pliable plants, of coastal and some interior habitats 2

2. **a.** Peduncle short (up to 3 times length of stipe), straight or curved, but not helically coiled. Fruit asymmetric ..... var. ***maritima***
   b. Peduncle elongating and becoming helically coiled by fruiting stage 3

3. **a.** Fruit symmetric or almost so when mature (may be asymmetric when immature) ..... var. ***spiralis***
   b. Fruit asymmetric, with a distinct 'offset' beak ..... var. ***longipes***

Variety *occidentalis*, which ranges from Alaska to Saskatchewan and Nebraska, with a generally interior distribution, is probably the most distinctive variety in this province. The large, dense, dark patches formed by its colonies on the beds of shallow lakes in the interior are conspicuous and identifiable even when in a vegetative state. They are found in water to 2 metres deep, deeper than that where other varieties are usually found.

The other varieties are more widespread around the Northern Hemisphere, variety *maritima* extending southward to South America and Africa. Varieties *longipes* Hagstroem and *maritima*, where distinguishable as such, are confined to tidal estuaries and lagoons on this coast, while var. *spiralis* is found in shallow waters in inland lakes of alkaline or brackish character, as well as in coastal lagoons (*see* map p. 151).

The Family ZANNICHELLIACEAE

Submersed rhizomatous or stoloniferous perennials with linear, alternate or subopposite leaves and stipular sheaths. Flowers unisexual, sometimes dioicous. Staminate flower of 1–3 stamens, sometimes with a rudimentary perianth (none in ours). Pistillate flower of 2–9 separate carpels, each with a single pendulous ovule. Fruit an achene, stipitate in ours, containing a seed without endosperm. Three genera; only one in North America.

The Genus *ZANNICHELLIA* L.

Horned Pondweed

Submersed perennial with often twining roots, slender rhizomes or stolons, and filiform leafy stems. Leaves alternate or subopposite, apparently in four ranks, narrowly linear to filiform, with one central vein, and with free stipular sheaths.

The pattern of stem growth involves a cycle of 3 successive internodes, only the first 2 of which elongate. Thus, of the three 2-ranked alternate leaves in the cycle, the first, which may be bladeless and represented by only a sheath, is obviously alternate, while the remaining two form a subopposite pair. Growth from axillary buds repeats the cycle but with the ranks at right angles to those below, producing a 4-ranked appearance. Above the third leaf, the stem terminates in a pistillate flower (Posluszny and Sattler, 1976a).

Flowers monoicous, unisexual, greatly reduced and lacking perianths in ours, terminal though appearing axillary due to the prolonged vegetative growth from the adjacent axillary buds. The staminate flower a single stamen terminating a short branch in the axil of the lower leaf of the subopposite pair. The pistillate flower of 2–5 (commonly 4) separate carpels with oblique, funnel-like stigmas. Pollination under water. Fruit a stipitate achene tipped with a stylar beak.

There are two species: one in Africa, and the following one.

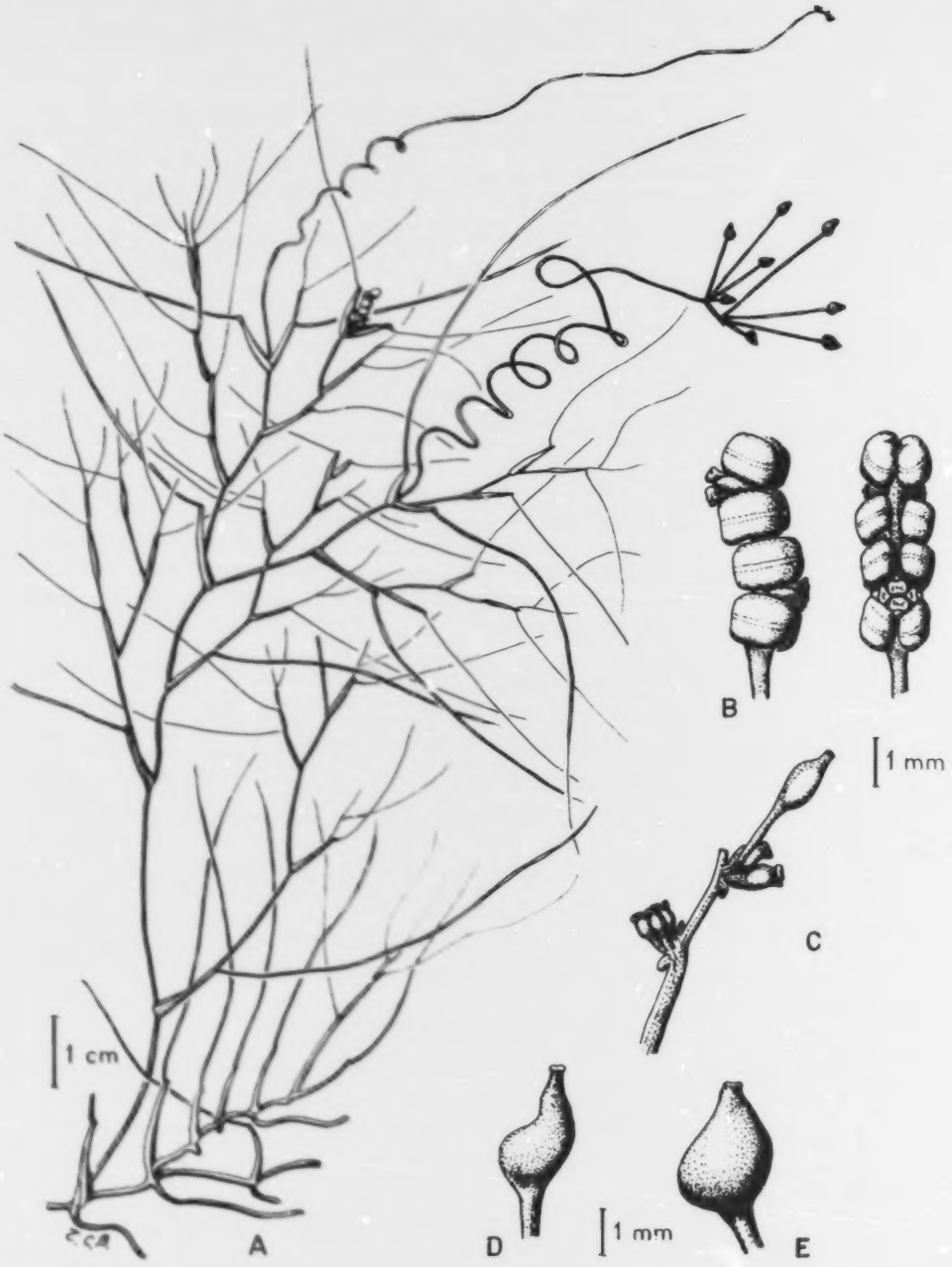


Figure 48. *Ruppia maritima* var. *longipes*: A, plant; B, flower spikes; C, spike after flowering, with one ovary fertilized; D, immature achene; E, mature achene.

***Zannichellia palustris* L.** **Horned Pondweed**

Freely branching, slender, rhizomatous or stoloniferous perennial up to 50 cm or more long. Leaves 2–10 cm long by ½–1 mm wide, with flaring sheaths free of the leaf bases and encircling the stem. The bladeless sheath that represents the first leaf of the stem cycle initially encloses the entire nodal complex of the shoot end. In the axil of the lower leaf of the subopposite pair, an axillary branch, that may also give rise to a lateral vegetative branch, terminates in a staminate flower consisting of a single stamen with two or four anther sacs and a protruding connective. The terminal pistillate flower, beside the axillary bud that gives rise to prolongation of growth, is short-stalked, surrounded by a perianth-like sheath, with normally 4 (rarely 2) carpels on short stipes, with prominent styles 1–1.5 mm long terminating in oblique peltate stigmas. Achenes spreading on widely diverging stipes, oblong, 2–3 times as long as thick, 2–4 mm long, with crested and toothed dorsal keels, and with prominent stylar beaks 1–2 mm long with more or less hooked tips formed from the stigmas.

A cosmopolitan species, widespread in British Columbia. Found in shallow (to 60 cm), often calcareous or brackish water of lakes, slow streams, or tidal marshes (*see* map p. 151).

The Family NAJADACEAE

Naiad or Water Nymph Family

Mostly annuals, with subopposite, 4-ranked (or occasionally falsely whorled) linear leaves with single veins and dilated sheathing bases with axillary scales.

Flowers solitary or paired in the leaf axils, of very unorthodox development (Posluszny and Sattler, 1976b), unisexual; the staminate flower a single subsessile anther enclosed in two membranous envelopes with lobed orifices, the inner envelope becoming adnate to the anther, the pistillate flower a single ovule terminal on the floral axis, and becoming enclosed by a pistil with a slender style and 2–4 linear stigmas. The outer envelope around the stamen and the pistil around the ovule are identical in form and development. Pollination occurs beneath the water surface. Fruit a membranous-walled achene tipped by the persistent style and stigmas, and filled by the elongate seed with a straight embryo and no endosperm.

The Genus *NAJAS* L.

Naiad

The only genus, of about 40 species, one in British Columbia.

***Najas flexilis* (Willdenow) Rostkovius and Schmidt** **Water Nymph or Naiad**

Submersed monoicous plant, 1–15 dm long, profusely branched with alternate branches, and having a tufted appearance.

Leaves in subopposite pairs, 1–3 cm long by 0.5–1 mm wide, gradually tapering to slender tips, finely toothed along the margins and with dilated, toothed, sheathing bases.

Flowers sessile or subsessile in the axil of the lower of the pair of subopposite leaves, single or a staminate and pistillate flower together. Anther with one pollen sac. Anchene 3–4 mm long with a stylar beak 1–2 mm long, tipped usually by 3 stigmas. Seed smooth and shiny, 3 mm long by 1–1½ mm thick.

Widespread across North America and in northwestern Europe. Submersed in clear, shallow (½ m) to moderately deep fresh to brackish water. Though typically an annual, this plant has been reported occasionally to survive over winter as the basal part of the plant, which produces new buds and shoots in the spring (Stuckey, Wehrmeister, and Bartoletta, 1978) (*see* map p. 152).

Where abundant, this is an important plant for waterfowl, which eat all parts of the plant.

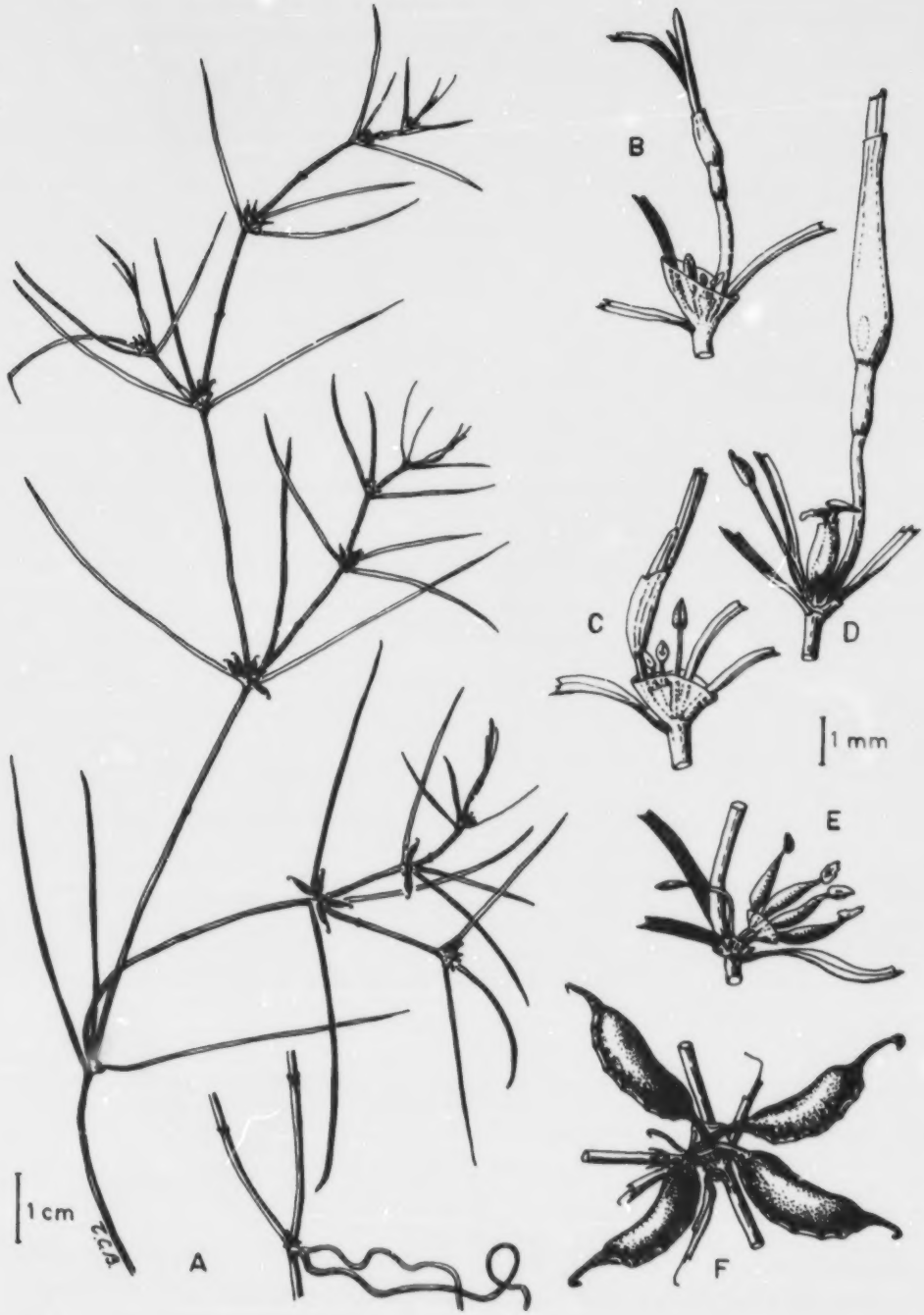


Figure 49. *Zannichellia palustris*: A, plant; B, young shoot tip, with immature staminate and pistillate flowers in sheath; C, node and sheath with later stage of flower development; D, node with mature flowers; E, developing fruits; F, mature fruits (achenes).

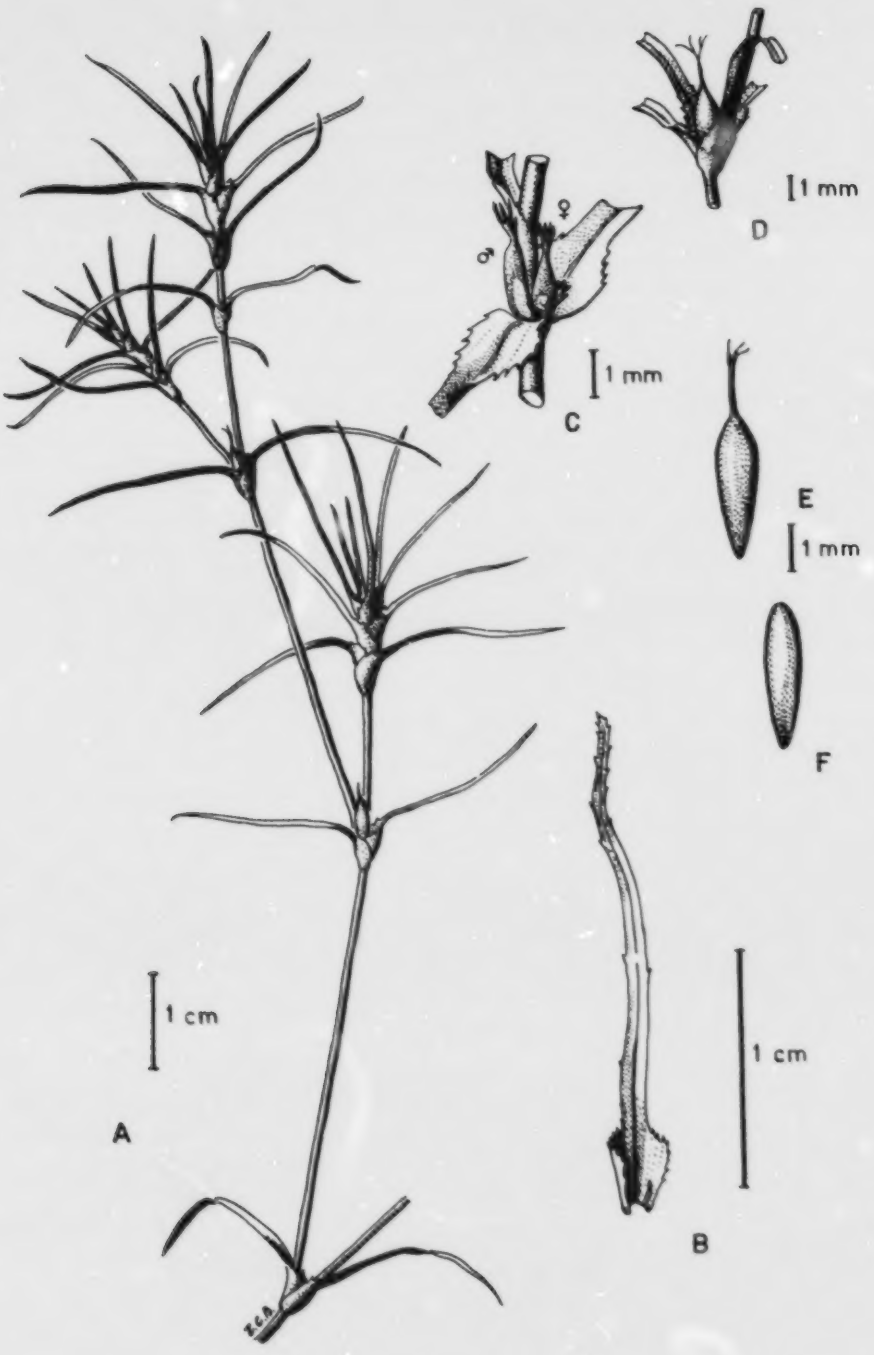


Figure 50. *Najas flexilis*: A, fertile shoot; B, leaf; C, node with staminate and pistillate flowers among leaf bases; D, node with fruit; E, fruit; F, seed.

The Family PONTEDERIACEAE

Pickerel-weed Family

Erect, trailing or floating perennials with rhizomes or stolons, sheathing leaf bases and bracts, and coloured flowers in spikes, racemes or compact panicles, rarely single.

Flowers complete, the joined bases of the perianth parts and the stamens forming a tube or funnel (hypanthium). Perianth parts coloured alike, often showy. Stamens 3 or 6, often of different forms or sizes. Carpels 3, connate but free from the hypanthium. Fruit a capsule or utricle. Seed with a slender straight embryo and abundant floury endosperm.

A small family, of six genera and 28 species, mostly tropical.

KEY TO GENERA

1. **a.** Erect, with cordate or oblong leaves. Flowers bilaterally symmetrical, blue in ours. Stamens 6, of unequal length ..... ***Pontederia***
   b. Submersed, trailing or floating, with lanceolate leaves in our species. Flowers, in ours, radially symmetrical, pale yellowish, and with 3 similar stamens ..... ***Heteranthera***

The Genus *HETERANTHERA* Ruiz and Pavon

Reclining, submersed, or floating plants with leaves of diverse form. Flowers solitary or in few-flowered racemes, the inflorescence initially enclosed in a spathe. Flowers with slender perianth-tubes and equally radiating tepals. Three stamens, one of them usually differing from the others. Fruit a capsule with several seeds.

About 10 species, mainly of warm regions of the Americas and Africa. Only the following species is found in British Columbia.

***Heteranthera dubia* (Jacquin) MacMillan** **Water Star-grass**

***Zosterella dubia* (Jacquin) Small**

Grass-like plant, commonly submerged except for the open flowers. Stem terete or rather flattened.

Leaves linear to lanceolate, sessile, the base adnate to the lower half of a tubular stipular sheath. Sheath with a conspicuous ligular extension that is at first rounded at the tip, but later breaks down, leaving two persistent fibres as slender appendages. Leaf blade tapering to base and acute tip. Leaves often subopposite where a flower arises.

Flower solitary, emerging from an axillary tubular spathe. Perianth tube long and slender. Tepals pale yellow, short-lived. Flowers often not opening, but self-pollinating in bud. Stamens 3, alike, with short flattened filaments and basally attached, sagittate-based anthers. Capsule unilocular, with several longitudinally ribbed seeds.

Ranging from southern Canada to tropical America. Found in shallow (to 1 m deep) water of lakes, ponds, or slow, sometimes muddy streams (*see* map p. 152).

The Genus *PONTEDERIA* L.

Pickerel-weed

Stout, emergent perennials with thick rhizomes and erect leaves and flowering shoots.

Inflorescence a compound spike, the flowers opening successively in each lateral spikelet. Hypanthium funnel-shaped; it and the perianth lobes minutely villous on the outer surface. Upper 3 lobes of the perianth coherent into a lip. Stamens 6, unequal in length; the anthers attached at their mid-points. Ovary 3-loculed, but only one locule fertile. Fruit a 1-seeded utricle enclosed in the distended hypanthium.

Three speices of temperate to tropical Americas. One known in British Columbia.

***Pontederia cordata* L.** **Pickerel-weed**

Leaves with stout, erect petioles and cordate, pinnately parallel-veined blades with rounded tips. Inflorescence dense, showy, the blue flowers puberulent on the outside, and with one or two yellow spots within on the upper lip of the perianth. Stamens very unequal: three projecting well out of the perianth tube, and three short, with their anthers in the mouth of the perianth tube. Anthers blue, rather heart-shaped. Fruit with six longitudinal toothed ribs.

Figure 51. *Heteranthera dubia*: A, flowering plant; B, stipular sheath; C, flower; D, seeds.

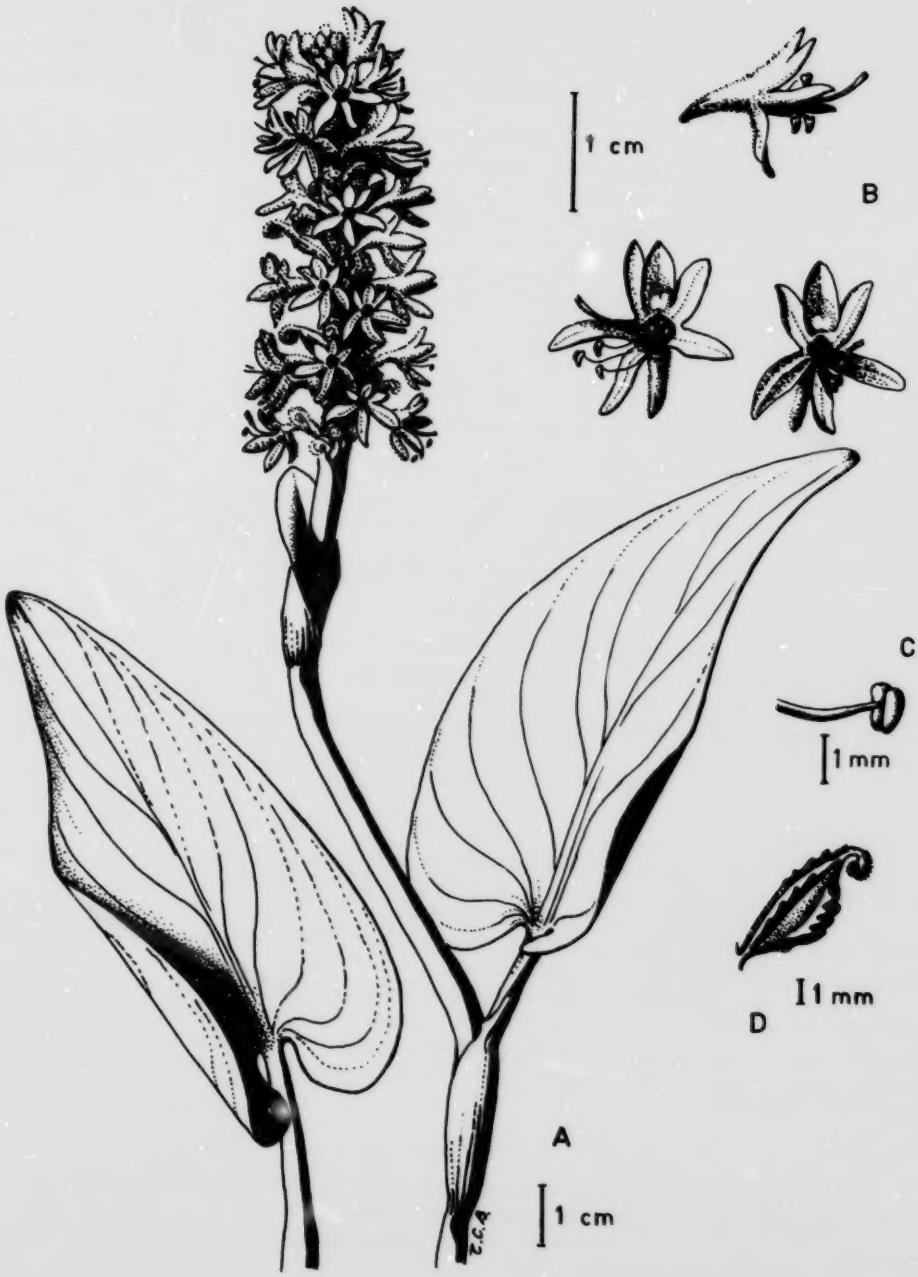


Figure 52. *Pontederia cordata*: A, upper part of flowering shoot, and leaves; B, flowers; C, stamen; D, maturing fruit.

Widespread in eastern North America. Introduced at Alberni, B.C., but not reported recently. It naturally grows in still lake water to a metre deep, and may form extensive colonies along the margins of shallow lakes (*see* map p. 153).

The Family ARACEAE

Arum Family

Perennial herbs (or vines, shrubs, or even small trees in the tropics) with acrid juice and bundles of calcium oxalate crystals (raphides) in many of the cells, stout stems or rhizomes, and commonly 2-ranked leaves with sheathing bases.

Inflorescence a densely flowered, axillary, often fleshy spike (spadix), subtended and, at first, usually enclosed by a conspicuous coloured bract (spathe). Individual flowers small, bisexual, or unisexual and monoicous, the ovaries and floral bases sometimes embedded in the fleshy body of the spadix; sometimes some flowers reduced to sterile appendages.

Fruit generally fleshy: either a cluster of berries, or a compound fruit composed of the fleshy spadix and the ovaries and seeds that are embedded in it.

A large family, of over 100 genera and about 1,500 species, mostly tropical and subtropical. Though the species in other parts of the world are generally terrestrial, or even epiphytic, the few species in British Columbia are all aquatic.

KEY TO GENERA

1. **a.** Leaves and spathes linear. Leaves set edgewise to the stem. Spathe green, never enclosing the oblique spadix ..... ***Acorus***
   b. Leaves and spathes broad. Spathe at first wrapped around the spadix **2**
2. **a.** Leaves net-veined, lanceolate to elliptic, very large, forming a rosette. Spathe yellow in ours ..... ***Lysichiton***
   b. Leaves pinnately closely parallel-veined, heart-shaped, 2-ranked. Spathe white ..... ***Calla***

The Genus *ACORUS* L.

Sweetflag

Aromatic plants with horizontal rhizomes and erect flowering shoots, the 2-ranked leaves set edgewise to the stem but sheathing at the bases. Spathe similar to a leaf, green, prolonged beyond the obliquely placed spadix, which it never encloses (an exception to the family character in this respect). Flower with 6 tepals and 6 stamens, greenish. Ovary 3-loculed, with several ovules. Fruit a spike of tiny dry capsules.

Two species; one known here.

***Acorus calamus* L.** **Calamus, Sweetflag**

Leaves up to a metre long by 2 cm wide, shiny, yellowish green, with their edges toward the stem above their sheathing bases, producing an iris-like impression.

Spadix projecting obliquely from the top of the peduncle, greenish, the erect, green, leaf-like spathe projecting up to 80 cm beyond the spadix, looking like a leaf-like extension of the peduncle. Spadix up to 9 cm long by 2 cm thick in fruit.

Widespread in the Northern Hemisphere; its geographical origin is now a little uncertain. It is generally, but not universally, thought to have originated in Eurasia, and been introduced into North America where it now occurs in widely scattered places, usually near settlements. It is found in marshy areas, commonly in shallow water (up to ¾ m deep), and may invade cat-tail (*Typha*) colonies (*see* map p. 153).

The Genus *CALLA* L.

Low, trailing perennial with 2-ranked leaves. Flowers without perianths; the lower ones on the spadix bisexual, with 6 stamens and a superior, unilocular ovary; the upper flowers consisting of stamens only. Fruit a cluster of berries, each with few to several seeds. Spathe opening wide.

Only the following species.

***Calla palustris* L.** **Calla**

Plant with long, horizontal, often floating or submerged green rhizome, the nodes giving rise to many long roots, and to alternate, 2-ranked leaves.

Figure 53. *Acorus calamus*: A, plant; B, surface of fruiting spadix.

Figure 54. *Calla palustris*: A, flowering shoot; B, fruiting spadix and spathe.

Leaves with heart-shaped, pinnately parallel-veined blades having acuminate tips, and petioles with ample stipular sheaths.

Spathe spreading, white, normally single, but rarely double or triple in forma *polyspathacea* Victorin and Rousseau. Flower spike white by reason of the crowded white anthers; the lower part of the spike punctuated by the projecting green pistils of the bisexual flowers. Berries red.

Circumboreal in distribution; mainly in the boreal and subalpine forest regions in British Columbia. Plants creeping in cold northern swamps, fens and marshy lake margins, often among emergent shrubby vegetation, at least some roots attached to shore or to some solid substratum (*see* map p. 154).

The Genus *LYSICHITON* Schott

Coarse perennials with large net-veined leaves. Spathe large; when open forming a hood around the spadix. Flowers all alike and complete, with 4 tepals, 4 stamens, and a 2-loculed inferior ovary largely sunk in the fleshy spadix body. Compound fruit formed of the rather fleshy spadix, with the many ovary bases, their locules and seeds, embedded in the compound mass.

Two species; ours and one in eastern Asia. The name sometimes spelt '*Lysichitum*'.

***Lysichiton americanum* Hulten and St. John** **Skunk-cabbage, Yellow Arum**

Rhizome short, thick, ascending, producing leaves in large rosettes. Leaves up to 1½ m long and ½ m wide, thin, netted-veined, tapering to usually relatively short winged petioles. Plant, especially when flowering, with a skunk-like smell.

Inflorescence appearing before the leaves in spring, and later overtaken by their growth. Spathe yellow, conspicuous, decaying after flowering is finished. Flower mass yellow at pollinating time, when the smell becomes particularly noticeable. Pollination is effected by small beetles. Fruiting spadix naked, pale green, rough-surfaced.

Plants of the western slope of Vancouver Island often have leaves with dark bluish green blotches and pale yellow spathes, and may flower when the leaves are comparatively well-grown.

Ranging from Alaska to California, and eastward to Montana; this species is widespread in British Columbia. It is found in swamps, wet forest, and wet meadows (*see* map p. 154).

The Family LEMNACEAE

Duck-weed Family

Tiny floating or submersed plants lacking any clear distinction between stem and leaf. Rootlets present or absent, bearing root-caps but no root-hairs. Raphides are found in some species, and axillary scales in a few species. Xylem tissue is commonly replaced by air channels (lacunae), and when it occurs, is unlignified.

Flowers minute, 2 or 3 together in a small pouch; normally one pistillate flower accompanied by one or two staminate flowers. Perianth none. Staminate flower a single stamen. Pistillate flower a single carpel with a short style, and containing one to several ovules. Fruit a 1- to several-seeded utricle.

The smallest flowering plants, members of this family show the ultimate reduction of the flowering plant in specializing for a floating aquatic life. Reproduction is almost entirely vegetative, flowers very seldom (never, in some species) being found. Vegetative reproduction is by budding of young plants directly from pouches in the edges or basal ends of older plants. By this means these plants can colonize small still ponds and ditches very rapidly, producing extensive floating patches of many thousands of tiny plants. Some species produce minute, rootless bulblets ('turions'), that sink to the bottom for the winter, and serve to regenerate the species vegetatively the following spring.

The *Lemnaceae* are a small worldwide family of four genera and 28 species. They are generally believed to be profoundly reduced relatives of certain small floating members of the *Araceae* (Daubs; 1965). Some species typically occur on eutropnic or polluted waters of limited extent.

Members of this family are eaten by waterfowl, and plants can be dispersed clinging to the feet or feathers of these birds.

Figure 55. *Lysichiton americanum*: A, plant at late flowering stage; B, fruiting spadix.

KEY TO GENERA

1. **a.** Roots absent. Plant body ellipsoid, about 1 mm long — ***Wolffia***
   b. Roots present. Plant body flattened, larger — **2**

2. **a.** Root one per plant body — ***Lemna***
   b. Roots several in a tuft — ***Spirodela***

The Genus *LEMNA* L.

Duck-weed

Plants of various shapes, usually flattened; each plant with one root hanging beneath it, and with two marginal reproductive pouches.

Flowers 3 (1 pistillate and 2 staminate) together, initially in a sheathing spathe, all in a marginal pouch. Anther 2-chambered. Ovary with 1–7 ovules. Fruit usually 1-seeded.

An almost worldwide genus of about ten species.

KEY TO SPECIES

1. **a.** Plant body broadly elliptic or nearly circular. Sessile or nearly so where attached to its parent plant — ***L. minor***
   b. Plant body narrowly obovate to lanceolate, distinctly stalked — ***L. trisulca***

Lemna minor L. *sensu lato*
Including *L. turionifera* Landolt

Plant disc-like, broadly elliptic, 2–5 mm long, green and smooth above, often purplish beneath, obscurely 3-veined, or seldom 5-veined, with a single rootlet attached centrally to the underside. Young plants stalkless or short-stalked, produced from a pair of marginal pouches near the basal end of the plant.

Fruit broadly flask-like, tipped with a short style, less than 1 mm long; $2n = 40$.

Almost worldwide in temperate to subtropical climates. Floating on the surfaces of ponds, forming bright green colonies of thousands of tiny discs; this is the most commonly seen of our duck-weeds.

Lemna minor L., in the broad sense, comprises a number of variants that have been distinguished as species. Two that are recorded for this province are *L. minor* L., *sensu stricto* and *L. turionifera* Landolt. They may be distinguished as follows (Landolt, 1975):

KEY TO SPECIES IN THE *LEMNA MINOR* COMPLEX

1. **a.** Plant 3–5-veined, without purple pigment beneath, with 1 or 2 papillae on the median line above, not producing rootless turions — ***Lemna minor sensu stricto***
   b. Plant 3-veined in North America, purple beneath with anthocyanic pigment, with 3–7 papillae along the median line above, producing rootless turions — ***Lemna turionifera***

Though the above distinctions appear to be clear in print, they are difficult to apply in practice. Pigmented and unpigmented plants may be found in one colony, sometimes even joined together in a vegetative mother-daughter relation. The papillae are hard to see except for the central one, the veins are often difficult to distinguish, and the turions are produced only under appropriate conditions, and thus are not normally found. Much of our material cannot be clearly assigned to either species at sight.

Lemna turionifera occurs across North America and in eastern Asia and Hawaii. Identifiable specimens at the British Columbia Provincial Museum are from Fort St. John, Burns Lake, Vanderhoof, Nakusp, and Osoyoos, B.C. Because of the uncertainty of distinguishing *L. turionifera* from *L. minor*, in the majority of cases, records of both are included in the distribution map for *L. minor*. (*see* map p. 155)

Lemna trisculca L.

Plant body rather elongate and lanceolate, tapering to a stalked base and to an acute apex, up to 13 mm long over all, dark green above and beneath, obscurely 3-veined. Pouches on either side near the junction of the stalk with the main plant body give rise to young plants, which spread at right angles to the axis of the parent plant. Several 'generations' of plants often remain attached to each other; $2n = 40$.

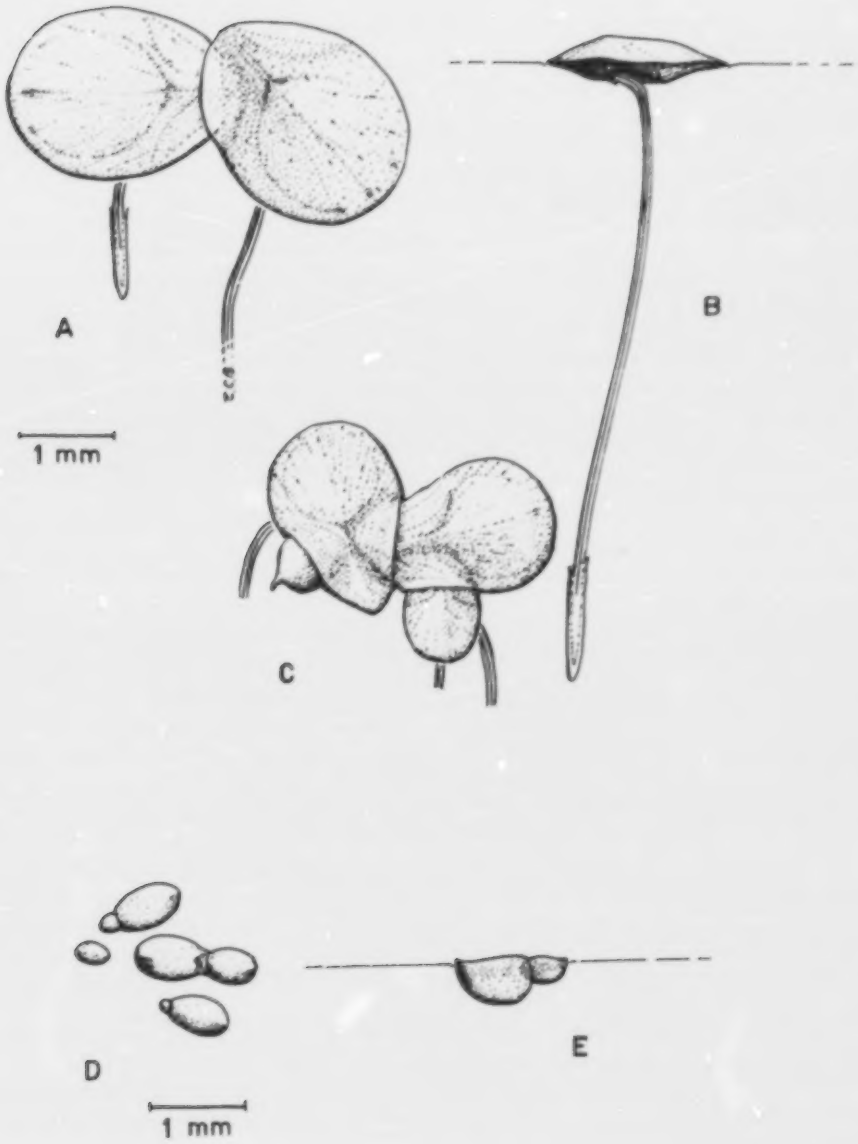


Figure 56. *Lemna minor* and *Wolffia borealis*: *Lemna minor* A, plant (top view); B, plant (side view); C, fruiting plant (top view). *Wolffia borealis* D, plants (top view); E, plant (side view).

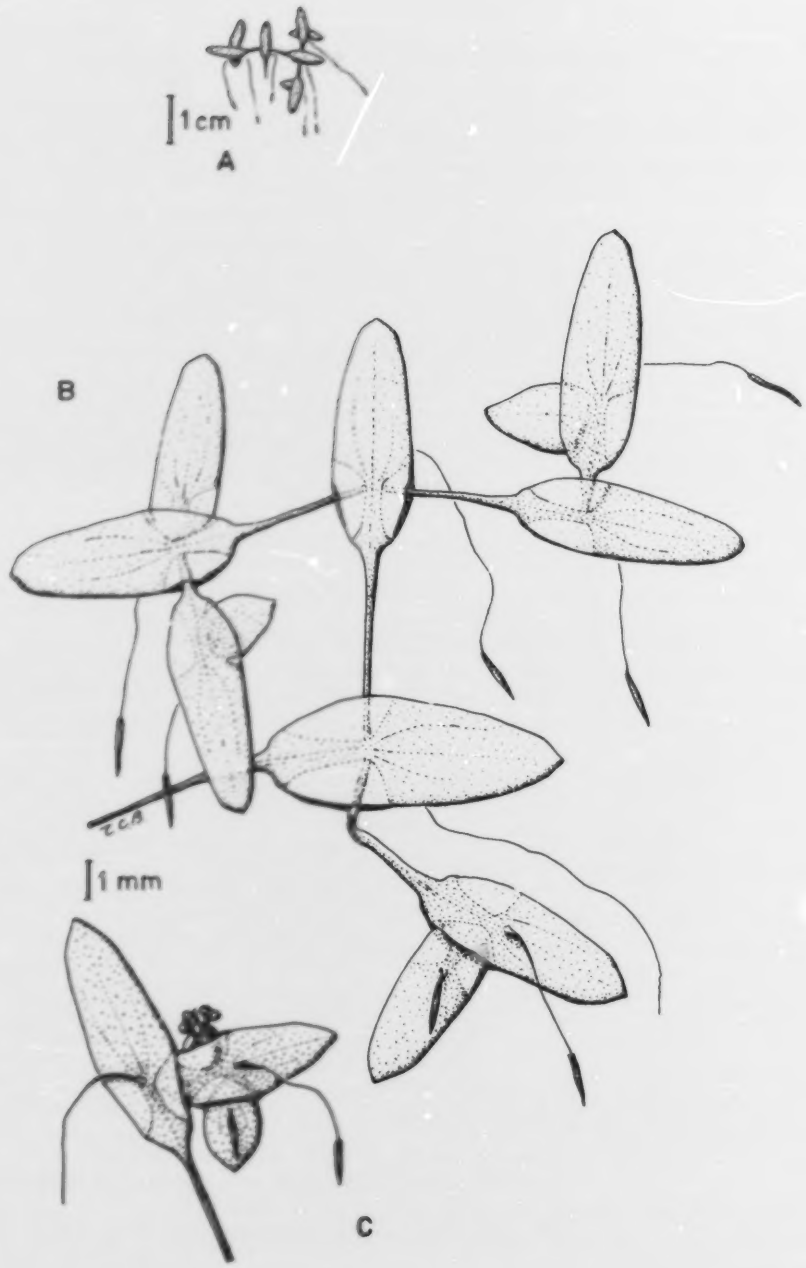


Figure 57. *Lemna trisulca*: A, small plant group (top view); B, plant group, enlarged, lower plant overturned; C, flowering plant (seen from beneath).

Widespread in temperate to subtropical climates. Less commonly seen here than *L. minor*. Plant commonly seen in still or slowly flowing, somewhat calcareous waters. This species may lie just beneath the water surface, forming looser-looking colonies than *L. minor*, or may lie at the bottom in water ½–2 m deep, forming extensive mats. Plants float exposed on the surface only for rare episodes of flowering (*see* map p. 155).

The Genus *SPIRODELA* Schleiden

Plant body discoid, broadly obovate, radially 5- to 12-veined, green above, purplish beneath, with a cluster of rootlets centrally attached beneath, and axillary scales.

Young plants arise in succession from a pair of baso-lateral submarginal clefts; the young plants stalked initially, but the stalk soon lost. A degree of asymmetry is shown by plants when in flower whereby one cleft (commonly the right hand one, as seen from above) is preferentially used for vegetative propagation, while the other gives rise to the flowers.

One pistillate and two staminate flowers are produced together in a membranous spathe in one of the submarginal clefts. Anther with 2 chambers, opening longitudinally. Ovary with 2 ovules.

A genus of 3 or 4 species, found on most continents, with one species here.

Spirodela polyrhiza (L.) Schleiden

Resembling a large *Lemna minor* plant as seen from above, the mature plant 4–8 mm long by up to 6 mm wide, dark purplish beneath. Rootlets 7–15, in a central tuft beneath.

Flowers enclosed initially in a sack-like membranous spathe in a submarginal pouch covered by a small flap.

This species produces small tubers or turions. These bodies are disc-shaped, 1–2 mm in diameter, veinless and commonly rootless, though they may develop a few short roots, and have one marginal reproductive pouch with a semi-circular translucent flap. They are olive green in colour, darker than a normal plant, with reddish dots, but with little or no purple colour beneath, thus contrasting with the growing plants, that sprout from them on short stems arising asymmetrically from the reproductive pouch. Turions may be produced during the growing season. Floating turions producing young, small plants, have been found in the Victoria area in early July; $2n = 40$.

Nearly cosmopolitan. Widespread in this province, but less abundant than *Lemna minor*. Found in the same habitats as *Lemna minor*, *Spirodela polyrhiza* reproduces much more sparingly, and seldom produces the large crowded colonies of that species. It commonly grows as isolated plants or small groups in *Lemna minor* colonies, where it may be distinguished by its conspicuously larger size (*see* map p. 156).

The Genus *WOLFFIA* Horkel

Water-meal

Plant body hemispheric or ellipsoidal, without veins or roots or raphides, and with one basal reproductive pouch that produces young plants in succession.

Flowers two together on the upper surface: one pistillate and one staminate; the anther 1-chambered; the ovary globular, with a very short style and one ovule. Fruit a globular utricle, the seed with scanty endosperm.

Six or seven species, mainly tropical and subtropical; only one known here. This genus contains the smallest of all flowering plants.

Wolffia borealis (Engelmann) Landolt and Wildi — Water-meal

W. brasiliensis Weddel var. *borealis* Englemann *ex* Hegelmaier

W. punctata auct. amer. non Grisebach

Plant ellipsoidal, 0.5–1.2 (average about 0.7) mm long and about half or less as wide, often faintly pale-dotted, with one pouch in the basal end, from which young plants arise in succession (Dore, 1957); $2n = 40$ (seldom 20 or 30) (*see* Fig. 56, p. 104).

Northeastern and western United States and southeastern Canada (Landolt, 1980), scarcely entering British Columbia.

At the few sites where the author has seen this species, the plant has formed a rich green 'cream' on the surface of a pond or ditch, far out-reproducing the accompanying *Lemna minor*, which was scattered in only small groups with it. This species, owing to its thick, not flat, plant form, has a gritty feeling when handled in the water (*see* map p. 156).

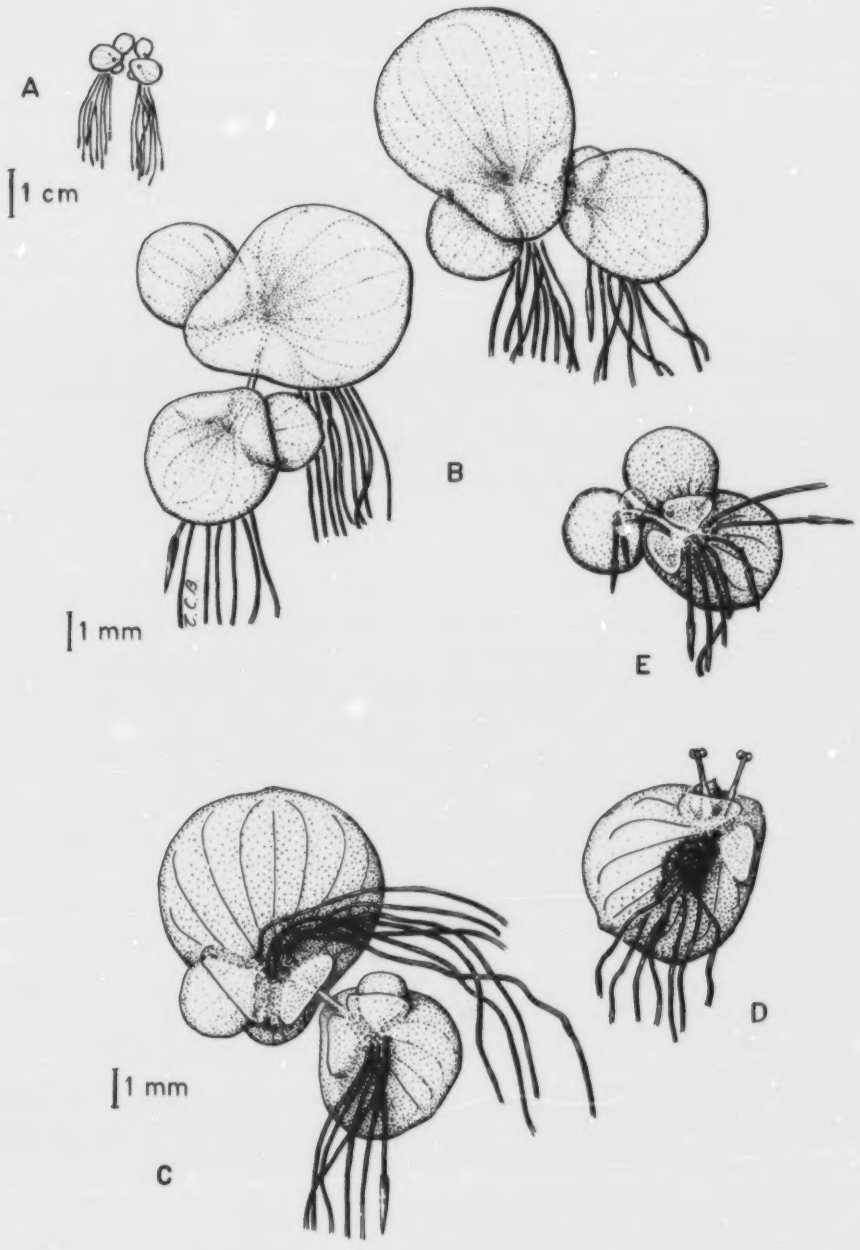


Figure 58. *Spirodela polyrhiza*: A, small plant group; B, plant group, enlarged, top view; C, plants seen from beneath; D, flowering plant (under view); E, germinating turion (on left) and first two "generations" of plants.

The Family TYPHACEAE

Cat-tail Family

Rhizomatous perennials with erect strap-like leaves and unbranched flowering stems. Xylem vessels present in conducting strands throughout the plant.

Flowers in very dense terminal spikes, the pistillate and staminate flowers in distinct segments of the spikes, the staminate flowers in the apical segment. Bracts of the inflorescence (one for each segment) usually transitory, dying and disintegrating early. Bracts of the flowers minute, hidden among the flowers, or absent.

Staminate flowers of 2–4 stamens, the filaments distinct or united. Pollen grains separate or coherent in groups of four (tetrads) when released. Pistillate flower with a perianth reduced to a tuft of hairs about as long as the pistil, and a 1-carpelled ovary on a stipe and tipped by a slender style and stigma, and containing one ovule. Sterile, stigma-less pistillate flowers are often mixed among the fertile ones.

The fruit, an achene released by the breaking away of the pistillate flowers from the axis of the spike, is light and buoyant by reason of the tuft of hairs, and is borne away on the wind. The seed with the embryo is embedded in endosperm made up of starch, oil and protein.

The family consists of one genus, *Typha*, of worldwide distribution.

The *Typhaceae* and *Sparganiaceae* are obviously closely related and, by some botanists (Thorne, 1976), are treated as one family, the *Typhaceae*. Their relationships to other Monocotyledons however, are more distant and obscure, and the subject of some disagreement; their combination with the *Arales* in a suborder *Ariflorae* (Thorne, 1976) being but one of a number of postulated assignments for them. Formerly included in the order *Pandanales*, they have been separated by recent workers from the *Pandanaceae*, which are characterized by multicarpelled, multiovuled ovaries and an arborescent habit of growth.

The Genus *TYPHA*

***Typha latifolia* L.** **Cat-tail**

Robust plant, 1–3 m tall, with a stout rhizome, the 2-ranked leaves pale greyish green, 8–20 mm wide, with inconspicuously sheathing bases.

Inflorescence with staminate and pistillate segments of the spike normally contiguous, but occasionally separated by a bare segment of stem. Pistillate flowers without bracts, with ovate to lanceolate stigmas. Sterile pistillate flowers club-shaped, rounded to apiculate with the short, aborted style above. Fruiting spike 1–3 cm thick, dark brown at maturity. Pollen grains released in tetrads; and borne away on the wind.

KEY TO FORMS

1. a. Spike segments contiguous ..... forma ***latifolia***
   b. Spike segments separated by a bare stem segment ..... forma ***ambigua***

The well-named forma *ambigua* (Sonder) Kronfeld may have narrower than average leaves and relatively slender spikes. Spikes of this form may characterize entire colonies or may be found scattered among normal ones. This form resembles *T. angustifolia* in gross appearance, and may be reported as that species. Microscopic examination of the pollen and stigmas may be necessary for definite identification of the species. *Typha angustifolia* has linear stigmas and separate pollen grains, and minute bracts among the pistillate flowers. This species has so far not been definitely identified in British Columbia.

Typha latifolia is widespread in the Northern Hemisphere, and is common in many parts of this province. It is a characteristic dominant of many shallow-water marshes. Multiplying and spreading by its rhizomes, it commonly forms extensive, dense colonies almost to the exclusion of other species (*see* map p. 157).

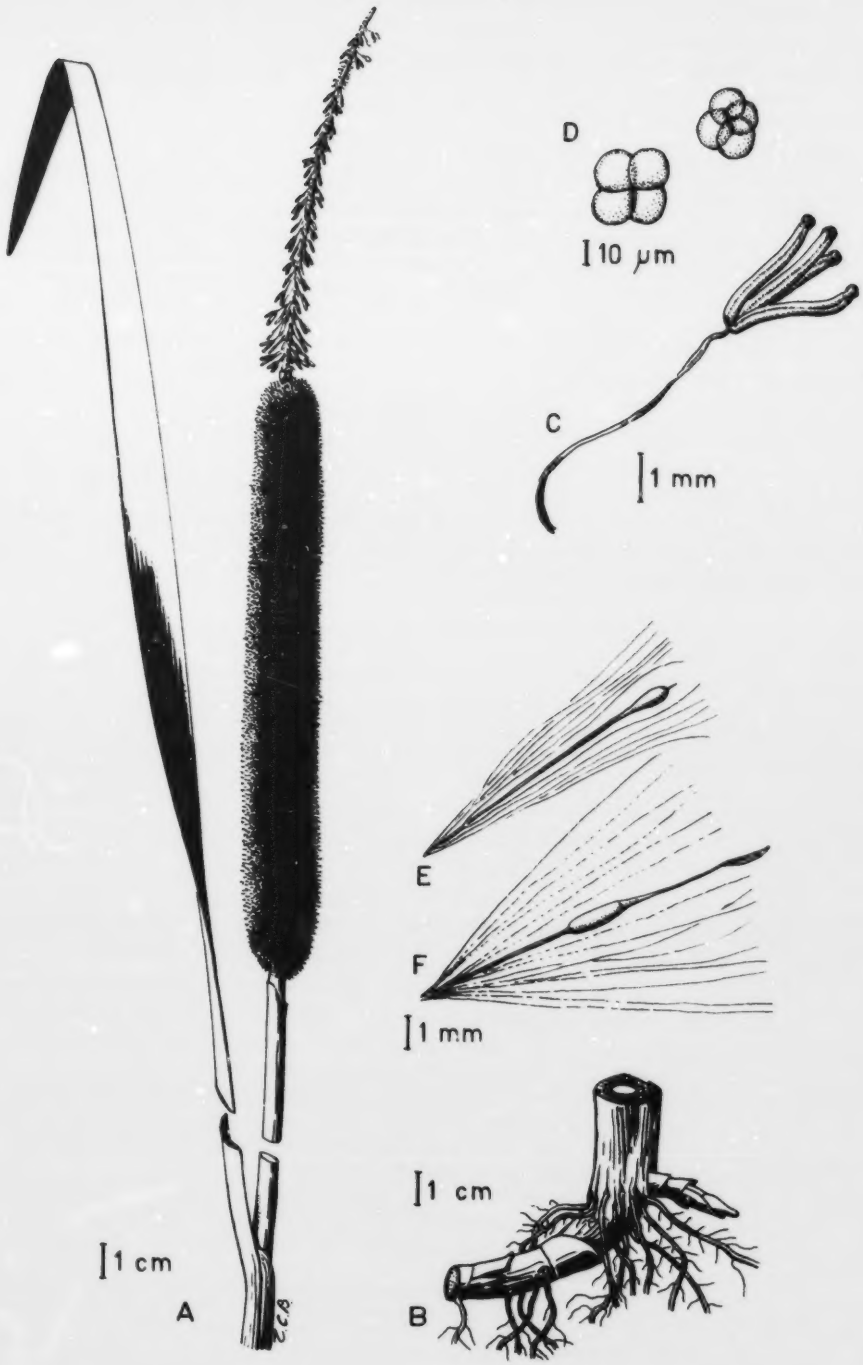


Figure 59. *Typha latifolia*: A, inflorescence at fruiting stage, and leaf; B, rhizome segment and base of shoot; C, staminate flower; D, pollen tetrads; E, sterile pistillate flower; F, fertile pistillate flower at fruiting stage.

The Family SPARGANIACEAE

Bur-reed Family

Aquatic, monoicous, rhizomatous perennials with alternate, linear leaves with sheating bases, and xylem vessels throughout the conductive tissues in the plant.

Staminate and pistillate flowers in separate globose heads, the pistillate heads below, and the staminate heads above, in simple or branched inflorescences, the pistillate heads at least subtended by conspicuous, leaf-like bracts. Some heads commonly appearing supra-axillary through fusion of axillary peduncles with the main axis of the inflorescence.

Staminate flowers individually almost indistinguishable, of 3–5 stamens surrounded by or mixed with several narrow scale-like tepals. Pistillate flowers short-pedicelled in most species, sessile in *S. eurycarpum*, consisting of up to six scale-like tepals and an ovary of one or two carpels, and bearing a beak-like style and one or two stigmas. Locules one or two, each with an ovule. Fruit an achene tipped by the stylar beak (often including the persistent stigma) and shed with the tepals attached. Seed with embryo embedded in starchy endosperm.

Assumed to be wind-pollinated, but bees have been seen visiting the flowers of some species.

The family consists of the one genus: *Sparganium*.

The Genus *SPARGANIUM*

Bur-reed

Characters of the family. Some sections of the genus have proven difficult to classify; the number of species described varies with varying treatment. The genus has about 20 species, mainly of the cool temperate regions of the Northern and Southern Hemisphere.

Sparganium species are very plastic in their character expressions. Superimposed on the range of genetically induced variation is variation in response to environmental factors such as altitude and water depth, and some apparently random variation for which no obvious cause can be distinguished.

Since they reproduce vegetatively by spreading rhizomes as well as by seeds, these species commonly form sizable colonies of "plants" that are in fact merely branches from a single original plant. Such a colony is a clone, with all shoots genetically identical. Even so, a surprising range of variation may be seen within a colony in such characters as leaf width and stiffness, and peduncle adhesion.

The plasticity in character expression in some species-groups, whether determined genetically or non-genetically, is a cause of much difficulty in identifying specimens and classification of the species is surprisingly difficult for a relatively small genus.

KEY TO SPECIES OF SPARGANIUM

1. a. Stigmas normally 2, 2 mm or more long. Fruit obconic or pear-shaped, sessile. Inflorescence branched, with many staminate heads, and pistillate heads confined to lateral branches. Anthers obovoid. Leaves stout, erect and arching, 8 mm or more wide ..... ***S. eurycarpum***

b. Stigma 1, under 2 mm long. Fruit tapering at both ends, stipitate. Inflorescence commonly unbranched. Anthers oblong or ellipsoidal. Leaves usually not more than 10 mm wide **2**

2. a. Staminate head usually 1, rarely 2. Achene beak 1.7 mm long or less. Stigma 0.8 mm long or less. Leaves usually floating **3**

b. Staminate heads 2—several. Achene beak over 1.5 mm long. Stigma usually longer. Leaves often upright **5**

3. a. All pistillate heads axillary, and usually sessile. Achene beak 0.5–1.5 mm long. Stigma 0.3–0.8 mm long. Leaves 2–8 mm wide, thin and translucent ..... ***S. minimum***

b. At least some pistillate heads supra-axillary. Lowest pistillate head usually peduncled. Leaves 1–20 mm wide, thick and opaque **4**

4. a. Achenes 3.5–4.5 mm long, beakless, or with a beak up to 0.5 mm long. Stigma 0.2–0.5 mm long. Heads usually clearly separate ..... ***S. hyperboreum***

b. Achenes 5–6.5 mm long, with a conical beak 1–2 mm long. Stigma 0.6–0.7 mm long. All but the lowest heads closely aggregated ..... ***S. glomeratum***

5. a. Pistillate heads all axillary or on axillary branches ..... ***S. americanum***

b. At least some pistillate heads supra-axillary **6**

6. a. Achene beak strongly curved and flattened. Stigmas ovate, 0.4–0.7 mm long. Anthers 0.8 mm or less long. Inflorescence often branched. Leaves floating or some erect ..... ***S. fluctuans***

b. Achene beak straight or slightly curved, terete. Stigmas linear, 1 mm or more long ..... ***S. angustifolium*** complex

***Sparganium americanum* Nuttall**

Slender or stout, usually erect and emergent plant. Leaves 3-angled, ascending and emergent, or sometimes ribbon-like and floating, 4–20 mm wide.

Inflorescence simple or branching. All pistillate heads, or branches bearing them, axillary. Main axis with 1–5 pistillate heads and 5–9 staminate heads. Branches, when present, with fewer heads.

Anthers 0.8–1.2 mm long. Stigmas 1–2 mm long. Fruiting heads 1.5–2.5 cm in diameter. Achene tapering to ends, dull or slightly lustrous, with a beak 1.5–5 mm long, including the 1–2 mm stigma.

Widespread in eastern North America, in shallow water and on shores. This close relative of the *S. angustifolium* complex (including *S. emersum*) is included here tentatively on the basis of reported occurrences in British Columbia by Fernald (1950), Boivin (1967), and Taylor and MacBryde (1977). Some rather ambiguous looking specimens, collected on Lulu Island in the Fraser River delta, and at Whiterock, with very short supra-axillary heads, have recently been identified by Vernon L. Harms as *S. emersum*. No material from British Columbia that is definitely assignable to *S. americanum*, is currently known to the author.

***Sparganium angustifolium* Michaux, Flora Bor. Amer. 2:18qx. 1803**
S. simplex* Hudson *nomen illegitimum
Including:
***S. simplex* var *angustifolium* (Michaux) Torrey**
S. simplex* var. *multipedunculatum* Morong (*S. multipedunculatumd*, (Morong) Rydberg) = *S. angustifolium* var. *multipedunculatum* (Morong) T. C. Brayshaw *comb. nov.
S. emersum* Rehmann, Verh. Naturf. Vereins Brünn 10:80. 1871 = *S. angustifolium* ssp. *emersum* (Rehmann) T. C. Brayshaw *stat. nov.
S. chlorocarpum* Rydberg North American Flora 17:8. 1909; = *S. angustifolium* var. *chlorocarpum* (Rydberg) T. C. Brayshaw *stat. nov.

Highly variable plant with creeping buried rhizomes. Stems slender and submerged to floating except for an emergent inflorescence, or erect and emergent.

Leaves in spring commonly floating and ribbon-like, up to a metre long. Later leaves may be floating, 2–5 (8) mm wide, convex dorsally, and dilated at the sheathing bases, or stiffly emergent, 2–5 dm long and up to 15 mm wide.

Inflorescence normally unbranched, the 3 or 4 pistillate heads normally peduncled except the uppermost, and at least one of them supra-axillary, its peduncle partially joined to the inflorescence axis. Staminate heads up to 8, the stamens white at flowering time. Anthers 0.8–1.5 mm long by 0.5 mm wide.

Fruiting heads 1–3 cm in diameter, greenish or brown. Achenes tapering to ends, sometimes with a median constriction; the body 3–5 mm long, on a stipe up to 2.5 mm long, and with a straight to slightly curved beak 2–5 mm long including the 1–2 mm long stigma. Tepals on the fruit 4–6, spatulate, fringed above, arising from the middle of the stipe and reaching about half way up the achene.

KEY TO SUBSPECIES AND VARIETIES

1. **a.** All leaves normally floating even on flowering shoots, and 5 mm or less wide, seldom wider, not translucent-edged. Stems normally submersed or floating, except for the inflorescence. Stigma about 1 mm long. Achene beak, including the stigma, 2–2.5 mm long. Bracts dilated at base ..... ssp. ***angustifolium***
   b. Spring leaves commonly floating, but flowering stems and their leaves normally upstanding out of water, and usually over 5 mm wide, often translucent-edged at base, and triangular in section. Stigma 1.5–2 mm long. Achene beak usually 3–5 mm long. ..... ssp. ***emersum*** ... 2

2. **a.** Bracts scarcely dilated at base. Leaves 3–8 mm wide ..... var. ***chlorocarpum***
   b. Bracts slightly to strongly dilated at base. Leaves 5–15 mm wide 3

3. **a.** Basal leaves strongly keeled at base, Y-sectioned. Mature fruit 12–15 mm long ..... var. ***emersum***
   b. Basal leaves not strongly keeled at base, V-sectioned. Mature fruit 10–12 mm long ..... var. ***multipedunculatum***

Figure 60. *Sparganium americanum*: A, upper part of plant, with fruiting inflorescence; B, fruit (achene, with attached tepals); C, stamen.

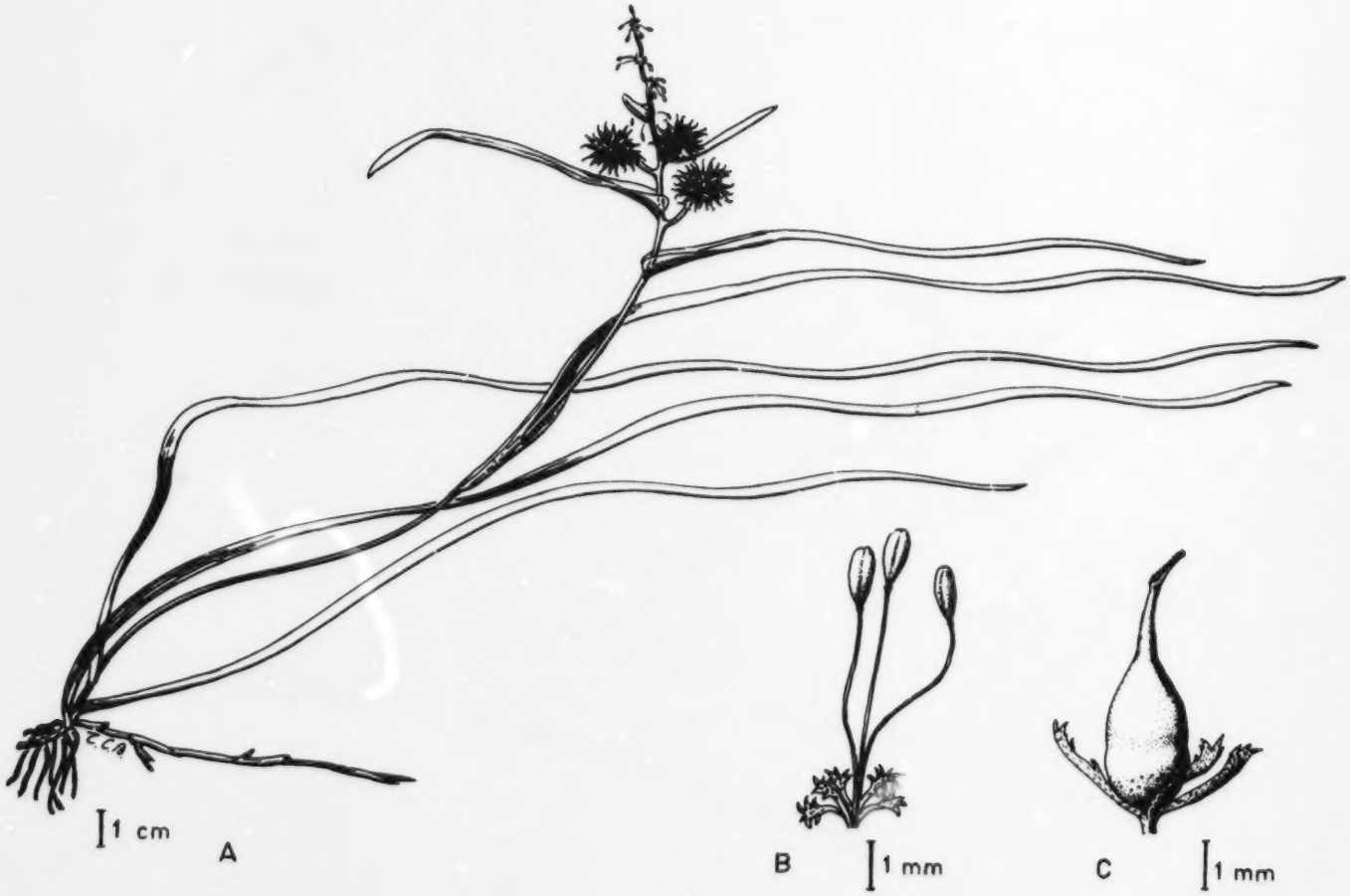


Figure 61. *Sparganium angustifolium* ssp. *angustifolium*: A, plant; B, staminate flower; C, fruit.

Figure 62. *Sparganium angustifolium* ssp. *emersum*: A, upper plant and fruiting inflorescence; B, fruit.

Both subspecies of *Sparganium angustifolium* are circumboreal in distribution. In North America they occur in one variety or another, over most of the continent, reaching south to California.

This species is found typically in cold ponds and ditches, with silt or muck bottoms, from the shore to water depths of a metre or more.

Subspecies *angustifolium* is quite variable in form. On Vancouver Island, plants appear more slender than normal. Especially at subalpine levels in the central part of the Island, they may have filiform leaves only 1–2 mm wide, and small heads only about a centimetre in diameter; thus they tend to resemble *S. hyperboreum* in gross appearance. The number of staminate heads, and the longer beaks and stigmas, indicate that they are *S. angustifolium* (*see* map p. 157).

***Sparganium angustifolium* Michaux subspecies *emersum* (Rehmann) T. C. Brayshaw *stat. nov.* (*Sparganium emersum* Rehmann, Verh. Naturf. Vereins Brünn 10:80. 1871. *S. simplex* Hudson *nomen illegitimum*)**

The distinction between subsp. *angustifolium* and subsp. *emersum*, while appearing clear when typical plants of these entities are compared, are rendered very indefinite when large populations are examined, because of the frequent occurrence of individuals of ambiguous identity that raise questions as to their origins and true positions in this complex. It is further suspected by this author, that ecological conditions may be involved, such that subsp. *angustifolium* may develop as a deep-water ecotype of subsp. *emersum*.

Hence the most practical treatment appears to be to combine these two 'species' as subspecies of *S. angustifolium*, whose name has priority (*see* map p. 158).

***S. angustifolium* Michaux ssp. *emersum* var. *chlorocarpum* (Rydberg) T. C. Brayshaw *stat. nov.* (*S. chlorocarpum* Rydberg, North American Flora 17:8. 1909)**

This entity was distinguished originally by Rydberg from *S. simplex* on the leaf characters mentioned in the above key, but whose expressions may be partly modified by water depth and other conditions, and by characters of the fruit (fruit 10–12 mm long, green, dull, with a stigma about 1.5 mm long, as opposed to fruit 12–15 mm long, brownish, shiny, with a stigma about 2 mm long in *S. simplex*) that may at least partly reflect the stage of maturity of the fruit. These differences, while often discernible, do not always correlate with each other. It is felt that the overall differences are not adequate to distinguish entities at the rank of full species, but rather to define varieties. Further, if the circumscription of *S. simplex* is taken as broad enough to include var. *multipedunculatum* (with fruit 10–12 mm long), as originally by Morong, it is broad enough to include var. *chlorocarpum*.

***S. angustifolium* ssp. *emersum* var. *multipedunculatum* (Morong) T. C. Brayshaw *comb. nov.* [*S. simplex* var. *multipedunculatum* Morong, Bull. Torrey Bot. Club 15:79. 1888. *S. multipedunculatum* (Morong) Rydberg, Bull. Torrey Bot. Club 32:598. 1905. *S. emersum* Rehmann var. *multipedunculatum* (Morong) Reveal]**

This variety, like var. *chlorocarpum*, has a transcontinental range in North America.

In *Sparganium angustifolium* and its relatives the degree of adhesion between the peduncles of the heads and the main axis of the inflorescence may vary widely and, when large populations of this species are examined, occasional individuals are sometimes found without any noticeable adhesion. These individuals, if considered in isolation from their natural companions, can be identified as *S. americanum* Nuttall. When such individuals are found in the field, they should be compared with other members of the colonies of which they are part, to see whether the lack of adhesion occurs systematically throughout the population, or whether it represents only the limit in one direction, in one individual, of a character that is more normally expressed in other members of the colony. Only in the former case should the name *S. americanum* be applied.

***Sparganium eurycarpum* Engelmann in Gray**
***S. greenei* Morong = *S. eurycarpum* var. *greenei* (Morong) Graebner**

Larger and coarser than our other species. Rhizomatous and colonial, the shoots always emergent and upright in habit. Stems coarse, up to 1.2, or rarely to 2 metres tall, commonly overtopped by the leaves, and branching from the upper axils. Leaves 1–2 cm wide, broadly triangular in cross-section, and keeled except at the tips.

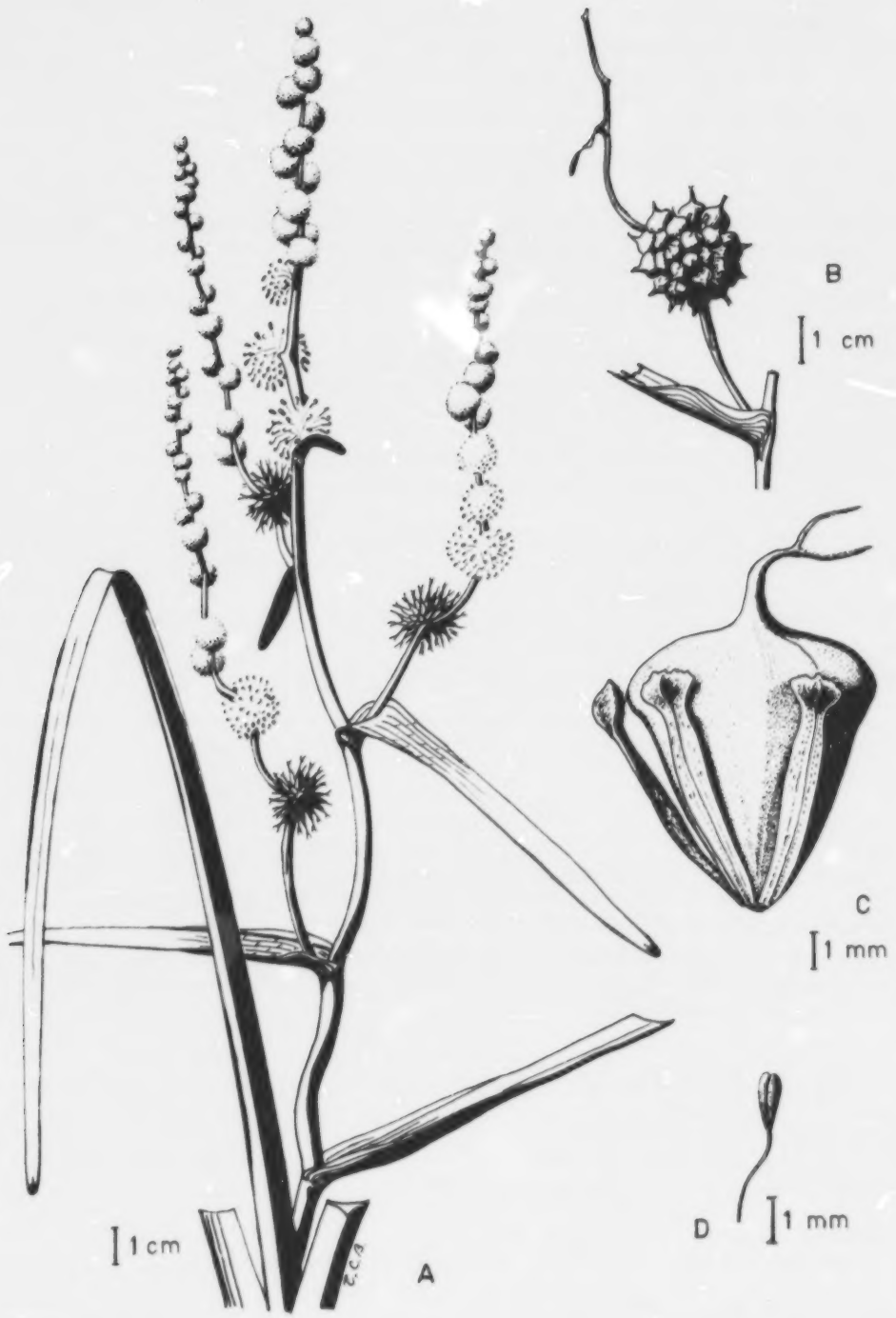


Figure 63. *Sparganium eurycarpum*: A, flowering shoot; B, fruiting head; C, fruit (achene with tepals); D, stamen.

Inflorescence large, branching, with few pistillate and many staminate heads, the green pistillate heads confined to low positions on the lateral branches and often absent from the main axis. All heads appearing sessile. Stamens 1 cm long, with white filaments. Anthers over 1 mm long, tapering and bluntly club-shaped. Pistillate flower sessile, with spatulate tepals more than half as long as the ovary and a normally bicarpellate ovary with two divergent stigmas 2 mm or more long.

Fruiting heads 2–3.5 cm in diameter, light yellowish brown. Fruit a sessile, relatively broad, top-shaped, usually 2-seeded achene, up to 1 cm long, with a rounded or subtruncate top narrowing abruptly to a stout beak 3–4 mm long; the stigmas, when persistent, add a further 2–3.5 mm.

KEY TO VARIETIES

1. **a.** Top of achene broadly rounded to truncate, with 2 stigmas ..... var. ***eurycarpum***
   b. Top of achene more narrowly rounded, or even tapering, commonly with only one stigma ..... var. ***greenei***

S. eurycarpum is widespread and transcontinental in North America; more common in the interior than at the coast, in British Columbia. Variety *eurycarpum* is found in shallow water, 20 cm to 1 m deep, around lake margins and in marshes, often where soils are clays, calcareous, or slightly basic. Variety *greenei* (Morong) Graebner (*S. greenei* Morong) ranges along the coast from southwestern British Columbia to California (*see* map p. 158).

Sparganium fluctuans (Morong) Robinson
S. androcladum (Engelmann) Morong var. *fluctuans* Morong

Slender perennial with stems up to 1.5 metres long, most of it usually submerged. Leaves elongate, ribbon-like, 3–11 mm wide, often floating, or the upper ones sometimes erect and emergent; the bases moderately dilated.

Inflorescence branching, with axillary or sometimes supra-axillary pistillate heads below and 3–4 staminate heads above on each branch. Anthers 0.4–0.8 mm long, elliptical. Pistillate flowers with tepals originating about the middle of the stipe or below, and barely reaching the middle of the mature achene. Stigmas narrowly ovate, 0.4–0.7 mm long.

Fruiting heads 1.3–2.3 cm in diameter. Achenes with strongly curved, flattened beaks 2–3 mm long, and often with a median constriction.

Cold ponds, lakes and slow rivers, often in relatively deep (1–2 m) water. Boreal North America from central British Columbia, where uncommon, to Newfoundland and northeastern United States (*see* map p. 159).

Sparganium glomeratum Laestadius

Stem rather stout, 1–6 dm long, upstanding or floating. Leaves stouter than in *S. hyperboreum*, 3–20 mm wide, floating or the upper ones emersed with the inflorescence.

Inflorescence with the lowest head distinct and supra-axillary, and the others aggregated at the top of the stem. Staminate head usually only one, and so close to the upper pistillate head that it appears to be sunk into it at the fruiting stage.

Fruiting heads 1–2 cm in diameter. Achenes 5–7 mm long overall, tapering into a short stipe and a conical beak 1–1.7 mm long, with a stigma 0.6–0.7 mm long. Scale-like tepals linear to oblanceolate, reaching about the middle of the achene.

A plant of water margins and shallow water, from Yukon and Alberta to Quebec and Minnesota. Rare in British Columbia (*see* map p. 159).

Sparganium hyperboreum Laestadius

Typically floating or submerged, with only the inflorescence emergent. Stem very slender and weak, and rhizomes similar. Leaves flaccid, 10–50 cm long by 1–5 mm wide, opaque, with funnel-like or tubular sheating bases, at least when young.

Inflorescence unbranched, of few heads. At least some pistillate heads supra-axillary, the lowest usually peduncled, the uppermost close to the usually single staminate head. Stamens 5–8 mm long, with broadly elliptic anthers 0.8 mm or less long. Pistillate flower unicarpellate, with a short ovate stigma 0.2–0.5 mm long, sessile or on a short beak up to 0.5 mm long. Tepals spatulate, a third to half as long as the ripe ovary.

Fruiting heads 5–13 mm in diameter. Achene beakless or with a beak up to 0.5 mm long.

Shallow water, to ½ m deep, commonly with a muck bottom; widespread in boreal regions of North America and Eurasia (*see* map p. 160).

Figure 64. *Sparganium fluctuans*: A, fruiting shoot; B, fruit; C, stamen.

Figure 65. *Sparganium glomeratum*: A, fruiting shoot; B, fruits.

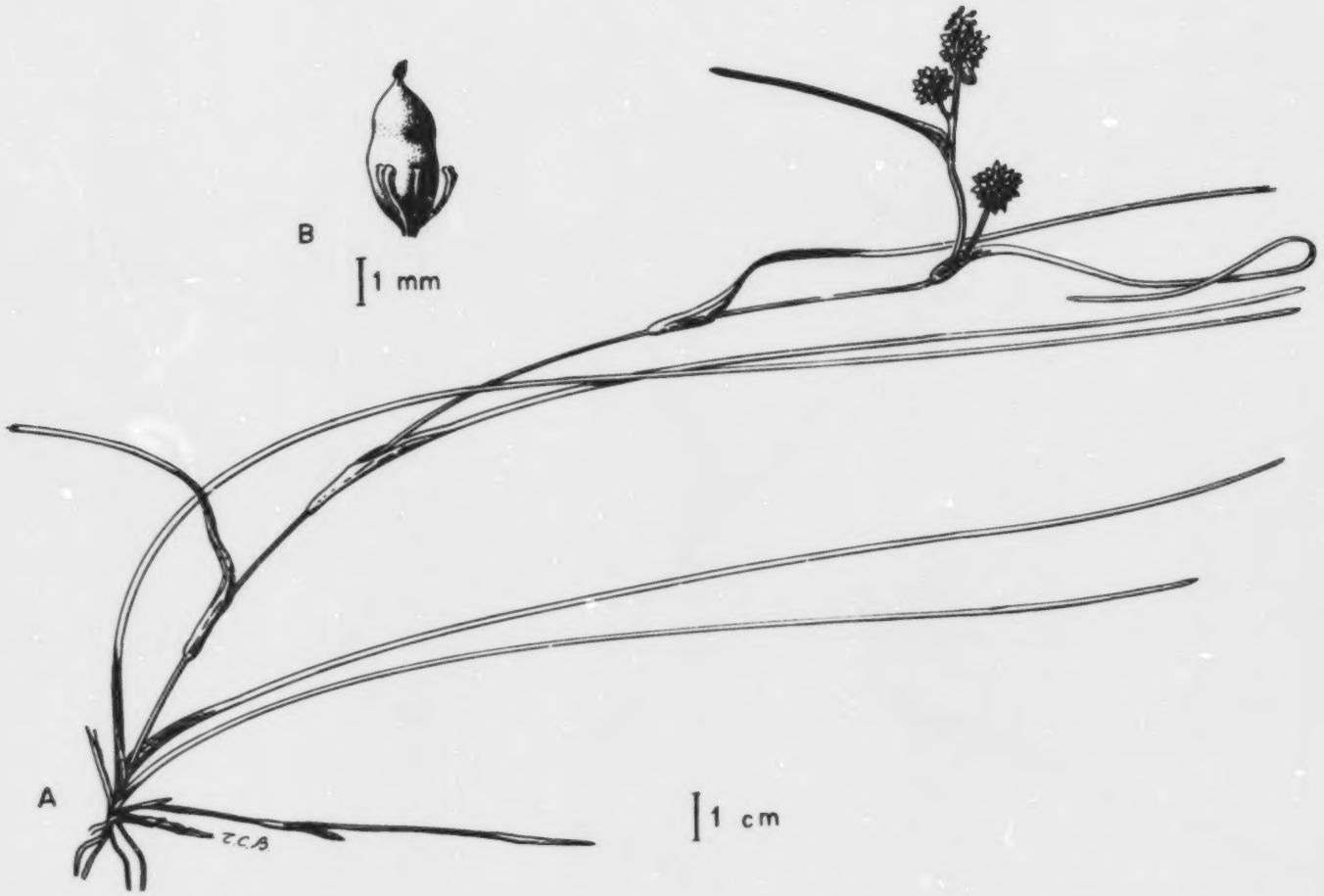


Figure 66. *Sparganium hyperboreum*: A, fruiting plant; B, fruit.

***Sparganium minimum* (Hartmann) Fries**

Similar in habit to *S. hyperboreum*, but with leaves 2–8 mm wide, flatter and often translucent, from sheathing bases with margins coherent when young.

Inflorescence unbranched, with all pistillate heads axillary and normally sessile though occasionally, peduncled, supra-axillary heads occur. Staminate heads one or rarely two, well separated from the uppermost pistillate heads. Stamens as in *S. hyperboreum* the anthers 0.8 mm long or less, and nearly as wide. Pistillate flower with spatulate tepals about half as long as the achene. Stigma elongate, up to 0.8 mm long, on a beak 0.5–1.5 mm long.

Fruiting heads 5–15 mm in diameter. Achene 3–4 mm long, with a distinct beak up to 1.5 mm long.

Habitat as for *S. hyperboreum*, found in water from 10 to 60 cm deep. Widespread circumboreal distribution (*see* map p. 160).

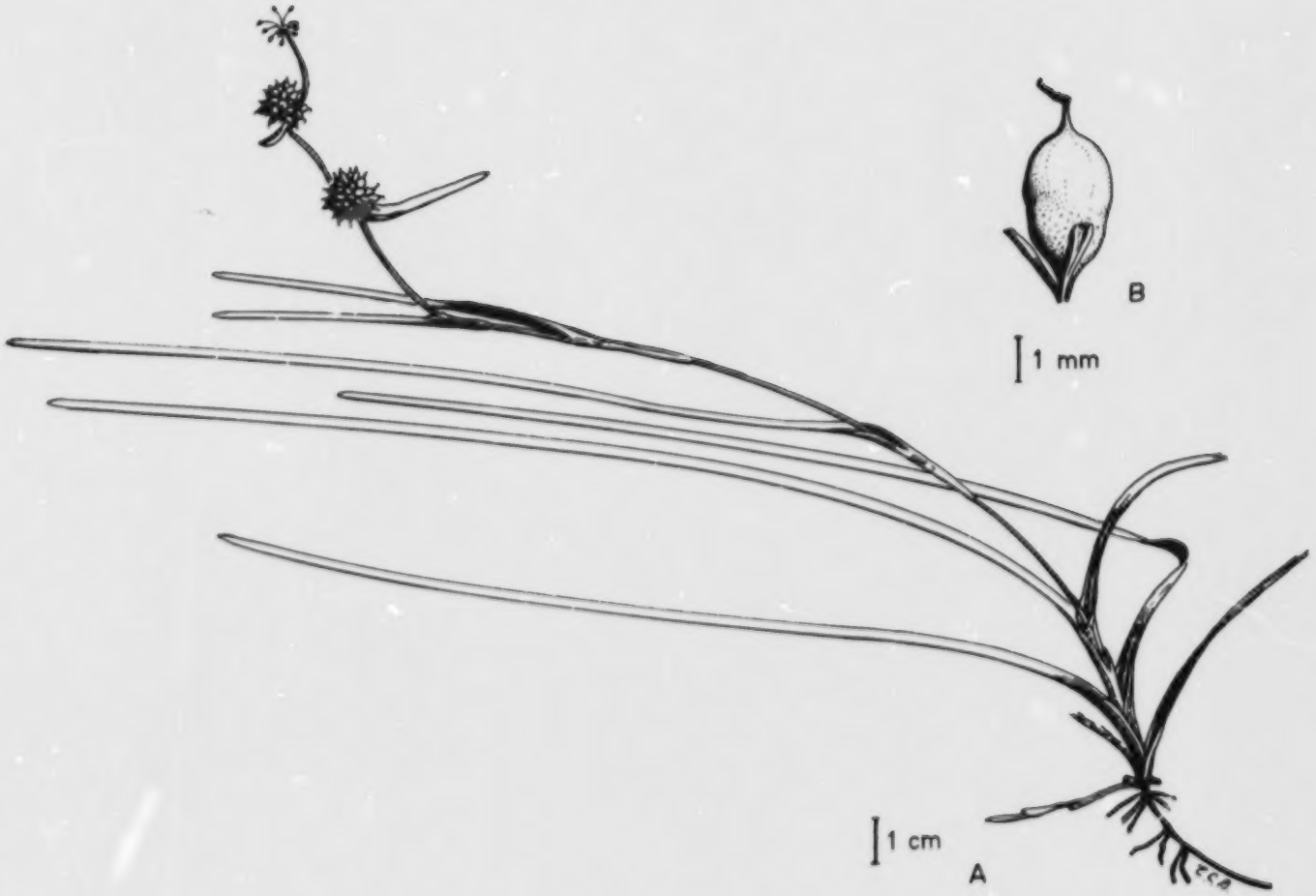


Figure 67. *Sparganium minimum*: A, fruiting plant; B, fruit.

GLOSSARY OF TECHNICAL TERMS USED IN THIS WORK

Several of the terms referring to structures of plants are illustrated in figure 68. These terms are indicated by asterisks. Plant names following some definitions indicate where these terms are illustrated in figures.

Achene—dry (i.e., non-fleshy) fruit containing one seed and not opening to release the seed (*Sagittaria*).

Acuminate (leaf apex)—narrowly tapering to acute tip.

Adnate—joined together, as applied to unlike organs (tepal + stamen in *Potamogeton perfoliatus*).

Alternate (leaves)—leaves arising singly at nodes: the usual arrangement in Monocotyledons.

**Anther*—pollen-containing body, often compound: the essential part of a stamen.

Anther-sac—one pollen-containing chamber in an anther.

Attenuate—tapering gradually to a drawn-out tip.

**Axil*—angle or gap above the point of attachment of a leaf or leaf stalk, and between that and the stem.

Axillary—placed in an axil, or arising from an axil.

Axillary scales—minute scales in the axil of, and attached to the base of, a leaf or leaf stalk (= '*squamulae intravaginales*' of technical manuals) *(Elodea nuttallii)*.

Baso-lateral (cleft)—situated at the side of a plant body near the basal end *(Spirodela)*.

**Bract*—a leaf, commonly reduced or otherwise modified, in the axil of which a flower or flower cluster arises.

Caducous—shedding early in the growing season.

**Carpel*—greatly modified leaf, enclosing one or more ovules: the fundamental unit of the pistil or ovary.

Cellular-reticulate—with epidermal cells arranged so as to form a regular net-like pattern with their cell walls.

Circumboreal—distributed all around the Northern Hemisphere in high latitudes.

Clone—population of genetically identical 'individuals' generated through asexual, vegetative means of reproduction, such as by rhizomes, tubers, offsets, or detached buds.

Connate—joined together, as applied to similar organs (carpels in *Triglochin*).

Convolute—rolled or lapped together, with overlapping edges, as petals in a flower bud.

Cordate—heart-shaped, as applied to leaf blade or leaf base *(Calla)*.

Cortex, cortical tissue—relatively unspecialized ground tissue in stems or rhizomes, in which vascular strands are commonly embedded, and which may be used for storage of food reserves. Its cells are often separated by intercellular air spaces (lacunae).

Cuneate (leaf base)—wedge-shaped, tapering.

Cuticle—waxy (or oily) waterproofing film coating the surface of the epidermis.

Cyme—inflorescence in which the terminal flower is the oldest, or is older than the nearby lateral flowers, and opens before them.

Cymose—having the developmental characteristics of a cyme (cymose panicle of *Alisma plantago-aquatica*).

Dehiscent (fruit)—splitting open to release seeds (follicles of *Butomus*).

Dentate (leaf margin)—with teeth that are equilateral, or at least not regularly oblique.

Denticle—very minute tooth (leaf margin of *Potamogeton illinoensis*).

Dioicous—having functional sexual structures (stamens and ovaries) on separate plants; often spelt dioecious.

**Dorsal keel*—keel or ridge on the edge of a fruit facing away from the flower axis *(Sagittaria cuneata)*.

Drupe—stone fruit: a fruit in which the seed is contained in a hard, nut-like shell (the endocarp) which in turn is embedded in a soft, fleshy or spongy outer husk (the exocarp).

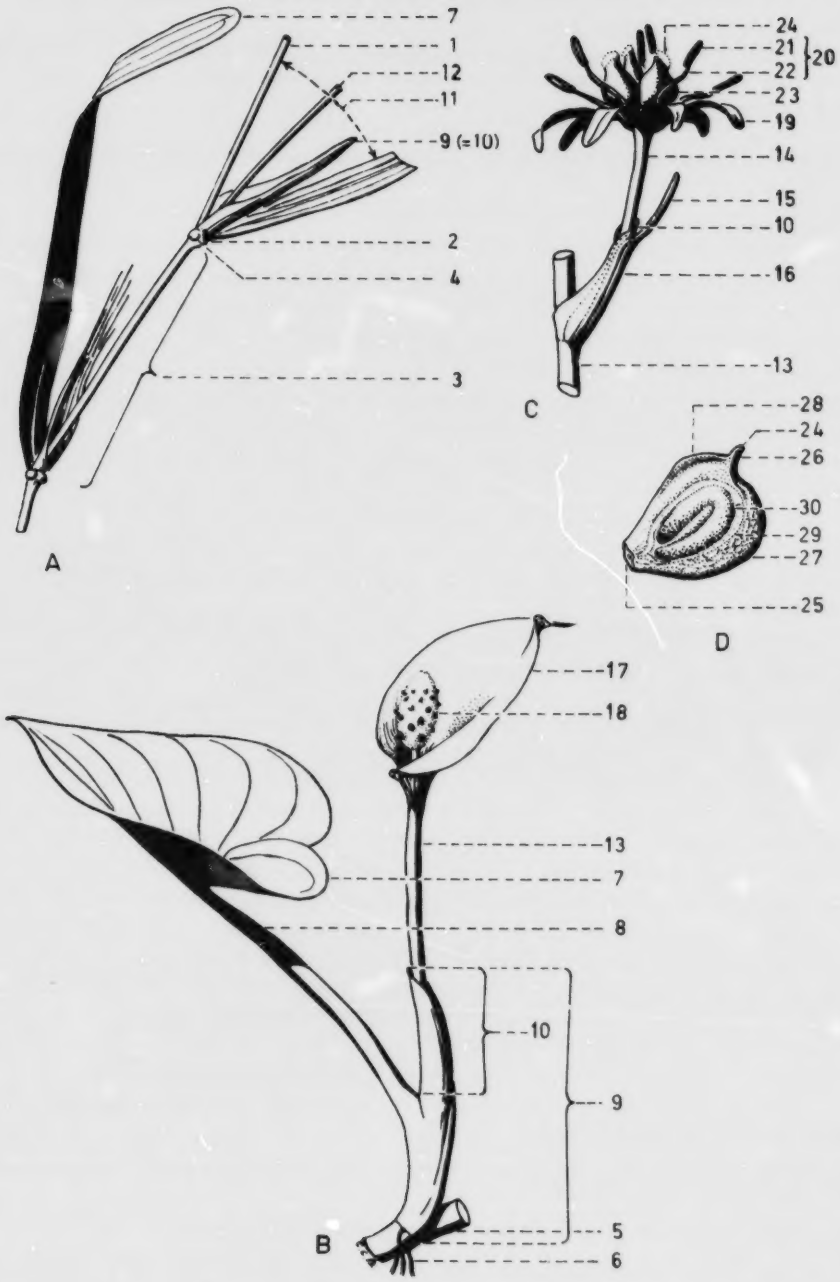


Figure 68. Structures Associated With Stems, Leaves, Flowers, and Fruits: A, stem and leaves of *Potamogeton obtusifolius*; B, leaf and inflorescence of *Calla palustris*; C, flower of *Scheuchzeria palustris*; D, fruit (achene) of *Sagittaria cuneata*.

Key to Structures: 1. main stem; 2. node; 3. internode; 4. nodal gland; 5. rhizome; 6. root; 7. leaf blade (lamina); 8. petiole (leaf stalk); 9. stipular sheath; 10. ligule; 11. axil of leaf; 12. axillary branch; 13. peduncle; 14. pedicel; 15. bract; 16. bract sheath; 17. spathe (expanded bract); 18. spadix (fleshy flower-spike); 19. tepal; 20. stamen; 21. anther; 22. filament; 23. carpel; 24. stigma; 25. basal scar (point of attachment to flower axis); 26. stylar beak; 27. dorsal keel; 28. ventral keel; 29. locule (seed chamber); 30. embryo in seed.

Ellipsoid—three-dimensional oval form, thickest at about the mid-point.

**Embryo*—the dormant embryonic plant within the seed *(Sagittaria cuneata)*.

Endosperm—food storage tissue accompanying, but not part of, the embryo in the seed.

Entire (leaf margin)—smooth-edged; lacking teeth or lobes.

Epidermis—outermost cell layer covering a plant (may be sloughed off older stems and roots).

Eutrophic (water)—having a high level of available nutrient chemicals.

Extrorse (anther)—anther attachment placing the anther on the outer side of its supporting filament, away from the axis of the flower.

Falcate—sickle-shaped (leaf of *Potamogeton amplifolius*).

False umbel—an apparent umbel, formed from a basically alternate branching pattern through failure of 2 or more internodes to elongate *(Butomus)*.

False whorl—an apparent whorl, formed from a basically alternate branching pattern through failure of 2 or more internodes to elongate *(Sagittaria)*.

Fertile (branch or shoot)—bearing flowers.

**Filament*—the part of a stamen supporting the anther.

Follicle—fruit formed of a carpel containing a number of ovules, and later, seeds; ultimately opening along one side to release the seeds *(Butomus)*.

Free (appendages)—separate; not joined to other appendages.

Fruit—seed-containing body; the product of the flower or ovary, or sometimes of a whole inflorescence.

**Gland*—small body, often projecting from plant surface: commonly for secretion of gums or other substances, but function not always known *(Potamogeton friesii)*.

Head—dense globular aggregate of sessile or subsessile flowers.

Hyaline—translucent.

Hypanthium—cup-like or tubular basal part of a flower, formed of the joined bases of the sepals, petals and stamens *(Pontederia)*.

Indehiscent (fruit)—not opening to release seeds.

Inferior ovary—ovary immersed in, and joined to, the base of a flower thus appearing to be below, or inferior in position to, the flower.

Inflorescence—a definitely structured aggregate or cluster of flowers.

**Internode*—segment of stem between two successive nodes.

Introrse (anther)—anther attachment placing the anther on the inner side of its supporting filament, toward the axis of the flower.

Keel—longitudinal projecting rib or ridge-like projection on a leaf or fruit (leaf of *Sparganium eurycarpum*, achene of *Sagittaria latifolia*).

Lacuna (pl. lacunae)—air chamber or passage among cells of cortical tissues of stems or of mesophyll in leaves. It may replace xylem in many aquatic plants.

Lacunate tissue—spongy tissue, containing extensive air passages (lacunae), developed in the cortex of a stem or mesophyll of a leaf, by enlargement of intercellular spaces or dissolution of cells to facilitate the diffusion of gases through the plant *(Potamogeton praelongus)*.

Lamina—leaf blade.

Lignification—process of formation of woody tissue (xylem), or of conversion of soft tissue into woody tissue, by deposition of lignin in cell walls.

Lignified—made woody by deposition of lignin.

**Ligule*—projecting upper part of basal stipular sheath of leaf above point of separation of sheath from leaf or leaf stalk *(Calla, Heteranthera)*.

Locule—ovule-containing chamber in an ovary; later the seed-containing chamber in the fruit.

Meristem—a 'growing tissue' where cell division and multiplication produce cells that subsequently develop into the various mature tissues to be added to the stem or leaf. Basal Meristem—meristem at the base of an internode of a stem, and causing the internode to elongate from the base, or at the base of a leaf, causing that to elongate: a common feature in Monocotyledons.

Mesophyll—green, chlorophyll-containing internal tissue in a leaf, specialized for functioning in photosynthesis.

Monoicous—having functioning sexual structures (stamens and ovaries) on the same plant, though not necessarily in the same flower.

Muck—sediment or wet soil with a very high content of decomposing organic residue.

Mucronate (leaf tip)—with small abruptly projecting tip on a rounded apex *(Potamogeton zosteriformis)*.

Netted-veined (leaf)—with largely non-parallel veins forming a netted pattern; typical of Dicotyledons, but unusual in Monocotyledons *(Lysichiton americanum)*.

**Node*—the point on a stem where a leaf or bract is, or has been, attached; normally a point of departure of a branch.

**Nodal gland*—gland situated at the node of a stem *(Potamogeton friesii)*.

Obconic—conical, but with the broadest end furthest from the point of attachment.

Obovate—two-dimensional form; egg-shaped in outline, widest near the distal end.

Obovoid—three-dimensional form: egg-shaped, thickest near the distal end.

Opposite (leaves)—leaves arising opposite each other in pairs at each node.

Orbicular—circular in outline (two-dimensional form).

Ovary—the lower, ovule-containing (and subsequently seed-containing) part of a pistil.

Ovate—two-dimensional, egg-shaped outline, widest near the basal end.

Ovoid—three-dimensional, egg-shaped body, thickest near the basal end.

Ovule—egg-containing body in the ovary; after pollination developing into the seed.

Panicle—diffusely branching inflorescence *(Alisma plantago-aquatica)*.

Parallel-veined—with veins lying closely parallel to each other, not obviously forming a net-like pattern; the usual arrangement in Monocotyledons.

**Pedicel*—stem bearing a single flower.

**Peduncle*—stem bearing an inflorescence.

Pedunculate (inflorescence)—borne on a peduncle.

Perfect (flower)—bisexual; having both functioning stamens and pistil in one flower.

Perennating—surviving over winter to the next growing season by vegetative (i.e., non-sexual) means.

Perianth—collectively the outer, or lower, sterile, whorls of a flower; i.e., the sepals + petals, or tepals.

Petal—member of the inner whorl of sterile appendages (perianth) of a flower.

**Petiole*—leaf stalk.

Photosynthesizing—synthesizing organic foodstuffs from inorganic raw materials (carbon dioxide and water), using the energy of sunlight.

Pinnately veined—with lateral veins departing successively from a main central midvein.

Pistil—the inner, ovule-bearing (and subsequently seed-bearing) part of a flower, consisting of the ovary, stigma(s), and often a style and formed from a carpel or a number of laterally coherent carpels.

Pistillate—pertaining to a flower in which only carpels function; functionally equivalent to 'female' in animals.

Pollination—the process of transfer of pollen from flower to flower.

Prophyll—in many Monocotyledons, the first leaf on an axillary branch, usually very reduced in size, often scale-like, situated in the angle between the branch and the main stem from which the branch has arisen *(Zostera marina)*.

Puberulent—with very fine, soft, more or less erect hairs.

Pubescent—downy with short soft hairs.

Raceme—inflorescence with equal-lengthed pedicels arising successively from a central axis *(Triglochin)*.

Raphides—minute clusters of calcium oxalate crystals in cells of *Araceae* and *Lemnaceae*.

**Rhizome*—a creeping, rooting stem, usually buried and horizontal, from which erect leafy and flowering branches arise *(Typha latifolia)*.

Rhizomatous—possessing a rhizome.

Sagittate—shaped like an arrow-head (leaf of *Sagittaria*).

Sagittate-based—with basal lobes shaped like the barbs of an arrow-head (leaf of *Sagittaria*, anther of *Heteranthera*).

Scape—a leafless stem arising from the base of the plant, supporting a flower or an inflorescence *(Alisma)*.

Schizocarp—fruit that at maturity splits into one-seeded carpels *(Triglochin)*.

Sclerenchyma—supportive tissue occurring as strands of elongate cells with very thick cellulose walls, providing mechanical strength without conduction of water or nutrients.

Sepal—one of the outermost sterile appendages of a flower, outside, or below, the petals.

Serrulate—with fine oblique saw-like teeth *(Potamogeton robbinsii)*.

Sessile—not stalked.

**Spadix*—a flower spike that is thick and commonly fleshy, often with the flower bases embedded in it; the whole often forming the fruit, as in *Araceae (Lysichiton)*.

**Spathe*—a bract, often large and coloured, that ensheaths a spadix, as in *Araceae (Lysichiton)*.

Spatulate—long and narrow, and broadened near the apex (tepals of *Sparganium eurycarpum*).

Spike—inflorescence in which sessile or subsessile flowers are attached directly to an elongate central axis *(Potamogeton)*. Compound spike is a spike of spikes *(Pontederia)*.

Staminate—pertaining to a flower in which only stamens function; functionally equivalent to 'male' in animals.

Staminode—a sterile, non-functional stamen, commonly lacking an anther (*Elodea canadensis* pistillate flower).

**Stigma*—apical surface on a pistil or carpel, specialized for the reception of pollen.

Stipe—elongated stem-like base of a carpel or ovary *(Ruppia)*.

Stipitate—elevated on a stipe.

Stipules—paired leaf-like appendages, or collar-like extensions of the base of a leaf stalk.

**Stipular sheath*—sheath formed from stipules, with or without attached petiole base.

Style—elongated extension of an ovary or carpel, bearing the stigma at its apex *(Butomus)*.

**Stylar beak*—beak on a fruit, formed from the style *(Potamogeton crispus)*.

Subopposite (leaves)—appearing opposite or almost opposite, commonly through failure of one internode to elongate between successive alternate, two-ranked leaves *(Najas flexilis)*.

Stoma (pl. *Stomata*)—pore in leaf epidermis to permit diffusion of gases between internal tissues and the outside air.

Superior ovary—ovary placed above, and separate from, the bases of the flower and of its appendages; the usual situation in this group.

Supra-axillary branch—branch appearing to depart from main stem above a leaf axil, due to union of base of axillary branch with the stem above the leaf axil (*Sparganium angustifolium*, pistillate peduncles).

Suture (of a carpel)—the seam, or edge of a carpel, where splitting may occur to release the seeds. Ventral suture is facing the axis of the flower, and is formed of the appressed margins of the carpel *(Butomus)*.

**Tepal*—sterile perianth appendage that is not differentiated as a sepal or petal.

Terete (stem)—cylindrical, and circular in cross-section.

Tetrad—group of four coherent pollen grains *(Typha latifolia)*.

Three-ranked (leaves)—alternate, and in three longitudinal ranks along a stem, every third leaf standing in the same rank; common in Monocotyledons.

Tracheae, vessels—tubular vessels in xylem, specialized for water conduction, and composed of large cells placed end to end, with the intervening partitions perforated, and the walls at least partly lignified. Characteristic of vascular systems of most flowering plants.

Turion—over-wintering shoot, branch, or winter-bud.

Two-ranked (leaves)—arising in two ranks along a stem, alternately to left and to right *(Potamogeton robbinsii)*.

Umbel—inflorescence in which all branches arise from one node at the apex of the peduncle.

Undulate (leaf margin)—wavy or undulating above and below the plane of the leaf *(Potamogeton crispus)*.

Unicarpellate (pistil)—consisting of only one carpel.

Unilocular (ovary)—having only one ovule-containing, or seed-containing, chamber, or locule.

Unisexual flower—flower in which only either stamens or carpels function, but not both.

Utricle—thin-walled, often bladder-like fruit containing a single seed *(Zostera marina)*.

Vascular strand—a clearly defined strand of vascular, conducting tissues running through stems, leaves or other organs; serving for transport of water, food, etc. The veins of leaves are vascular strands.

Vascular tissues—tissues specialized for conduction of water, nutrients, etc.; commonly for support; the essential tissues of stems and leaf veins.

Vegetative shoot—non-flowering shoot.

Vegetative reproduction—reproduction of plant from plant without recourse to sexual process; e.g., by tuber, rhizome, or winter-bud.

Ventral—facing toward the axis of stem or flower.

**Ventral keel*—keel or ridge on the edge of a fruit facing the flower axis *(Sagittaria cuneata)*.

Versatile (anther)—centrally attached and balanced on the end of the filament *(Pontederia)*.

Vessels—see Tracheae.

Vestigial—reduced to a minute vestige of original, larger, form.

Villous—with long, soft, curly but not matted, hairs.

Whorl—three or more leaves or branches arising around a stem at one node *(Elodea canadensis)*.

Whorled—arranged in whorls.

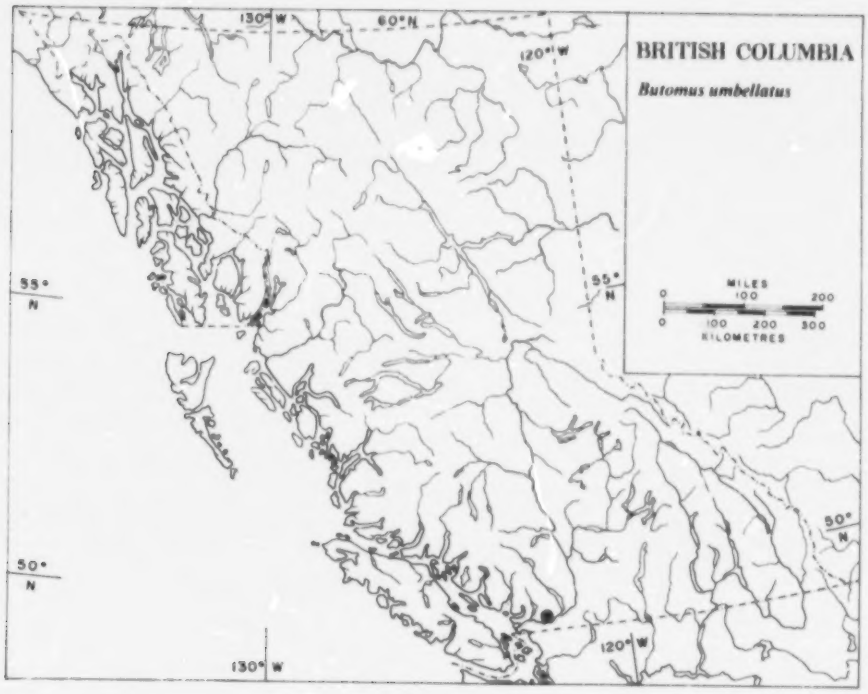
Wind-pollinated—having pollen carried on the wind from flower to flower.

Winged (stem)—having longitudinal flanges or projecting edges *(Potamogeton crispus)*.

Winter-bud—a bud, produced late in the growing season, that is shed, to lie dormant over winter and sprout in spring to produce a new plant (a turion).

Xylem—tissue specialized for water conduction, and rigid support in many land plants, having long thin cells with tapering ends, and usually with walls stiffened with lignin; the fundamental tissue of wood.

Maps Showing Points at Which Collections of the Species Discussed Have Been Made in British Columbia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MILES
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KILOMETRES
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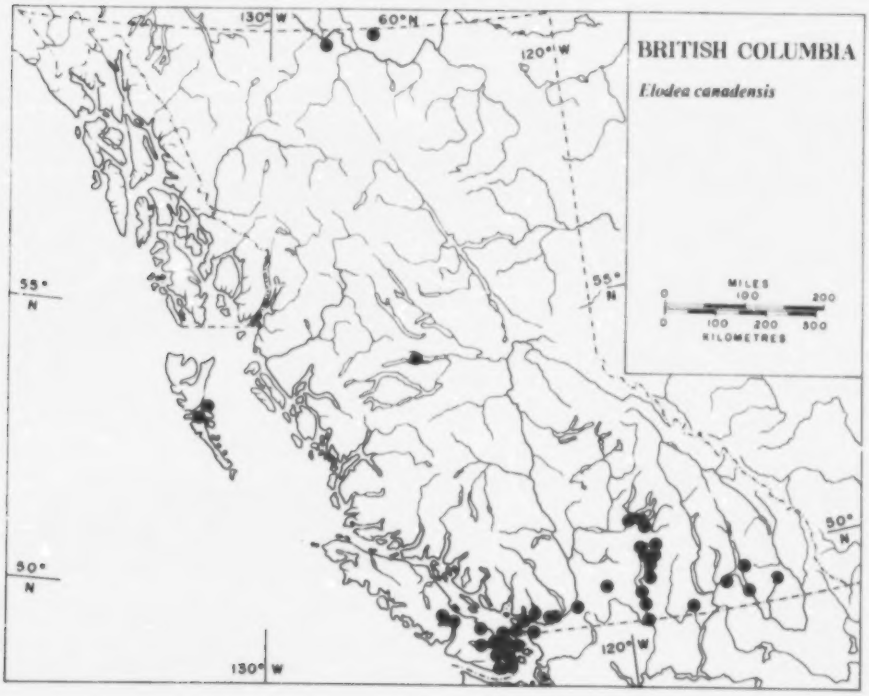
55° N
50° N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Elodea canadensis
MILES
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KILOMETRES
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120° W
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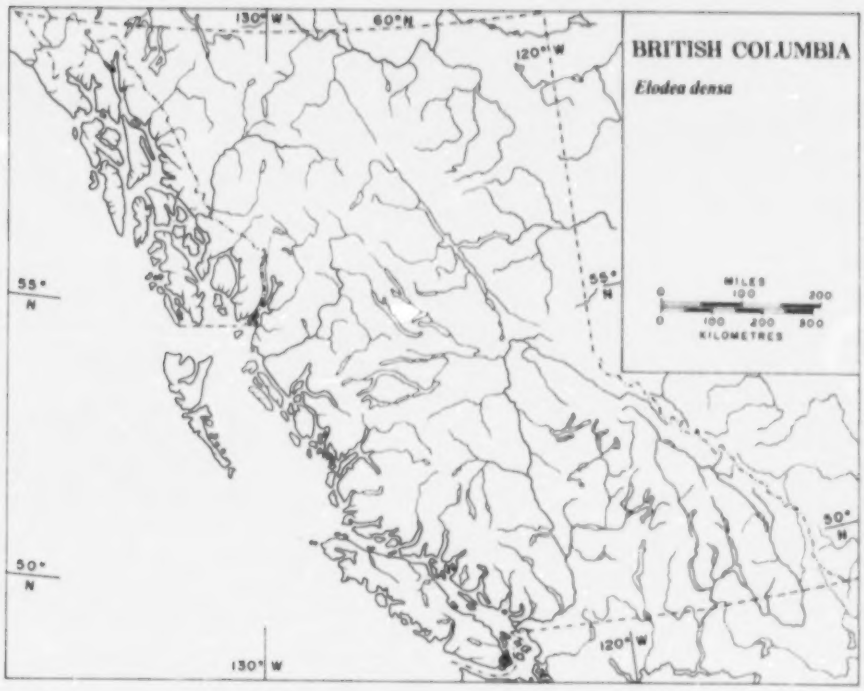
50° N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Elodea densa
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55° N
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MILES
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200
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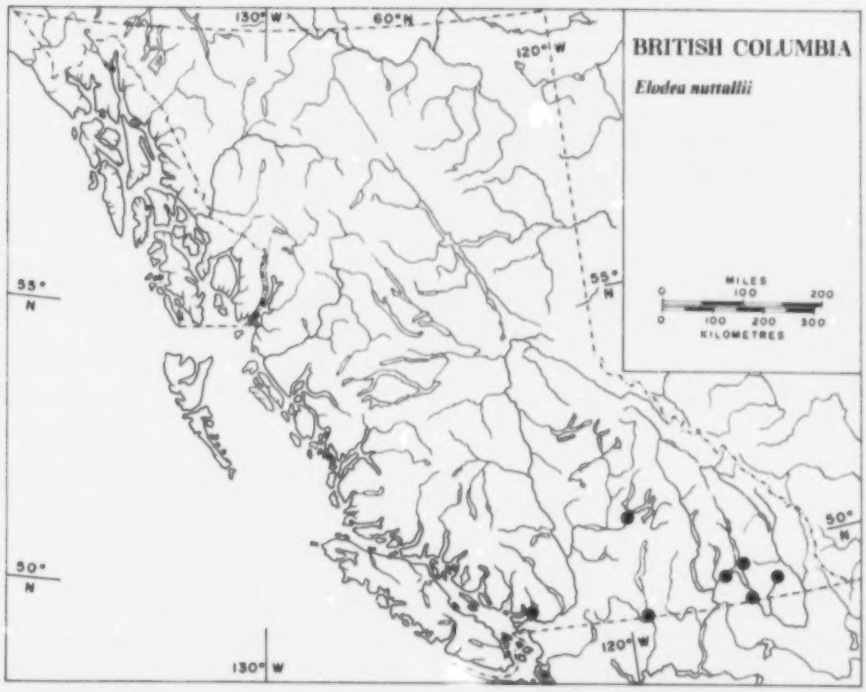
100
200
300
KILOMETRES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Elodea nuttallii
130° W
60° N
120° W
55° N
50° N
MILES
100
200
0
100
200
300
KILOMETRES

BRITISH COLUMBIA
Vallisneria americana
MILES
0 100 200
0 100 200 300
KILOMETRES
60°N
130° W
120° W
55° N
50° N

BRITISH COLUMBIA
Scheuchzeria palustris
MILES
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0 100 200 300
KILOMETRES
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130° W
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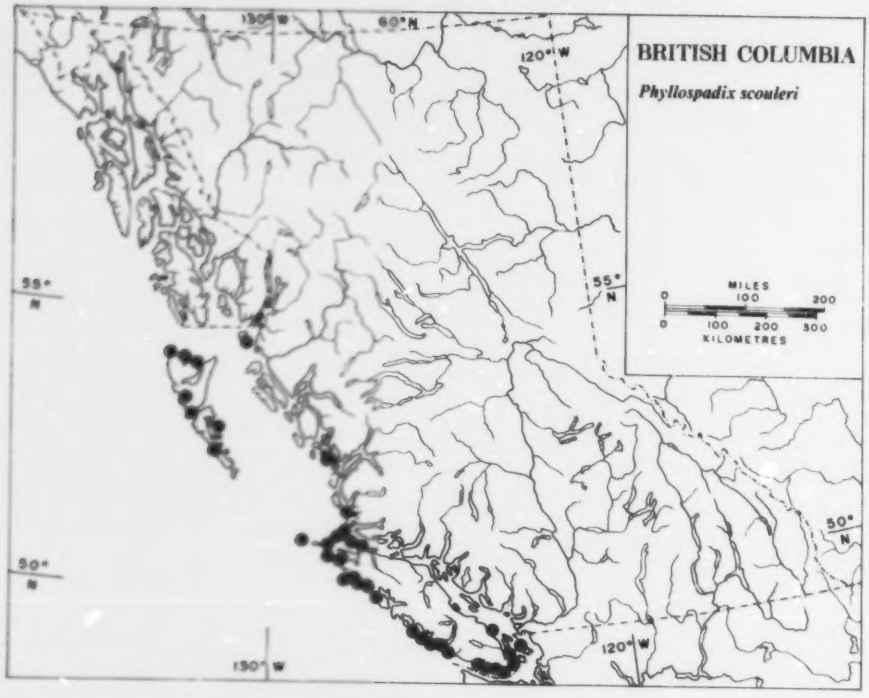
50° N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Phyllospadix scouleri
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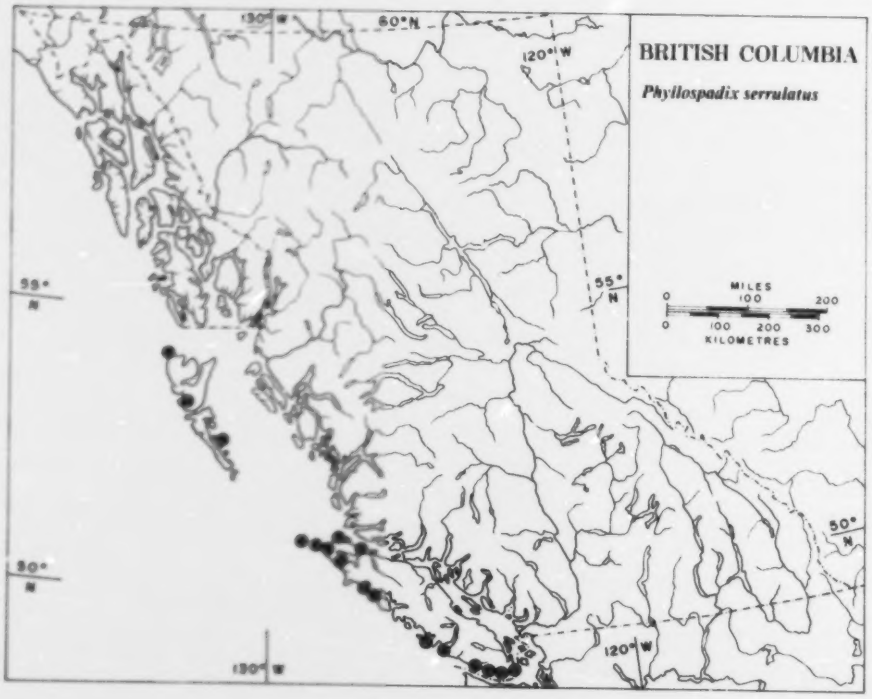
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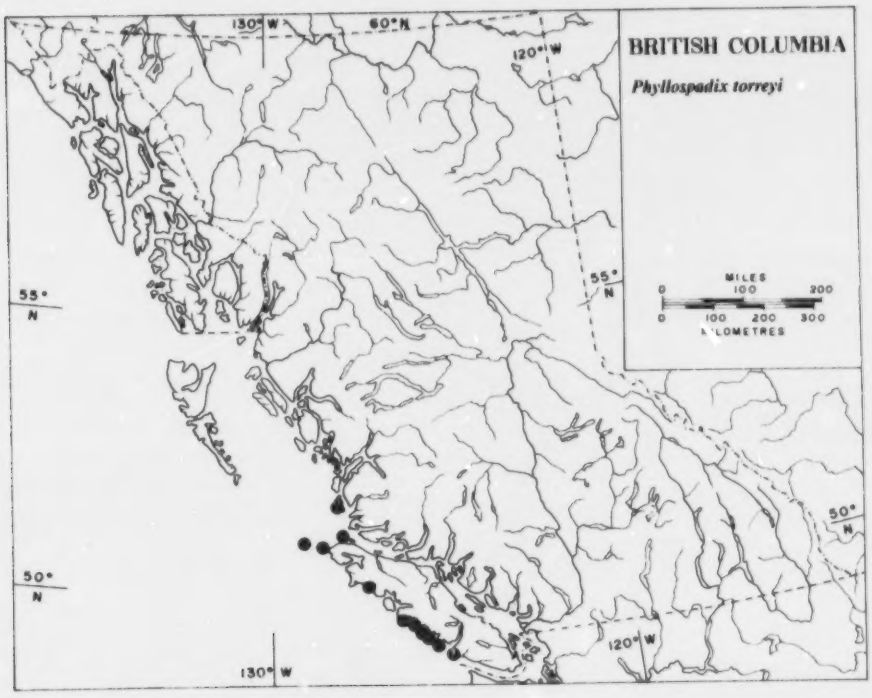
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Phyllospadix torreyi
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KILOMETRES
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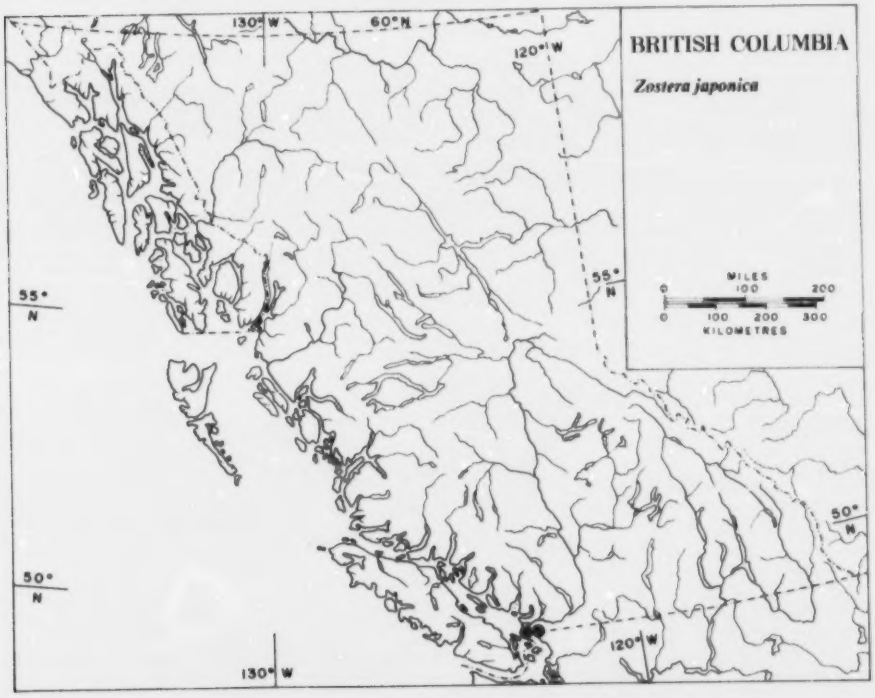
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KILOMETRES
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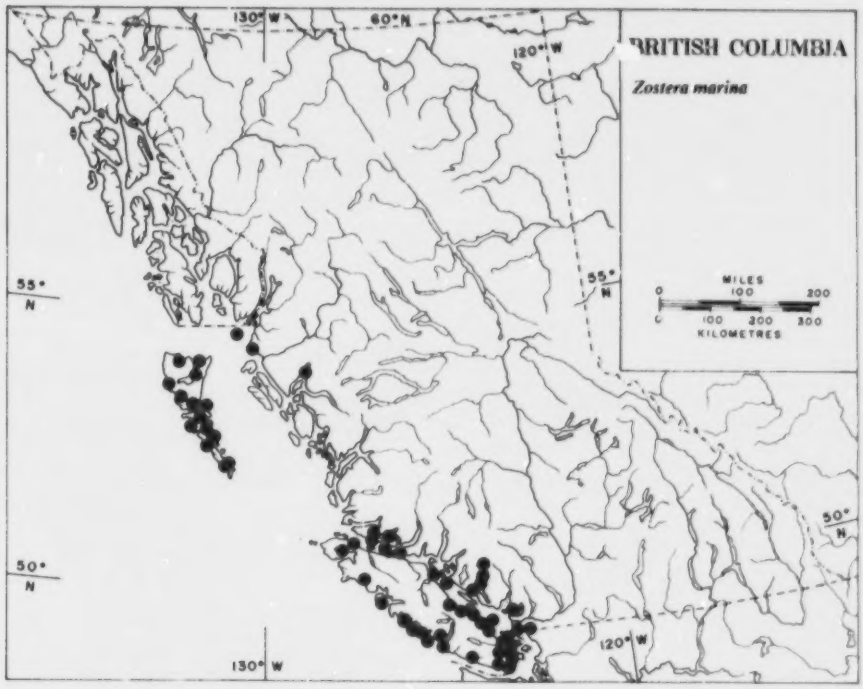
130° W
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BRITISH COLUMBIA
Zostera marina
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MILES
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KILOMETRES
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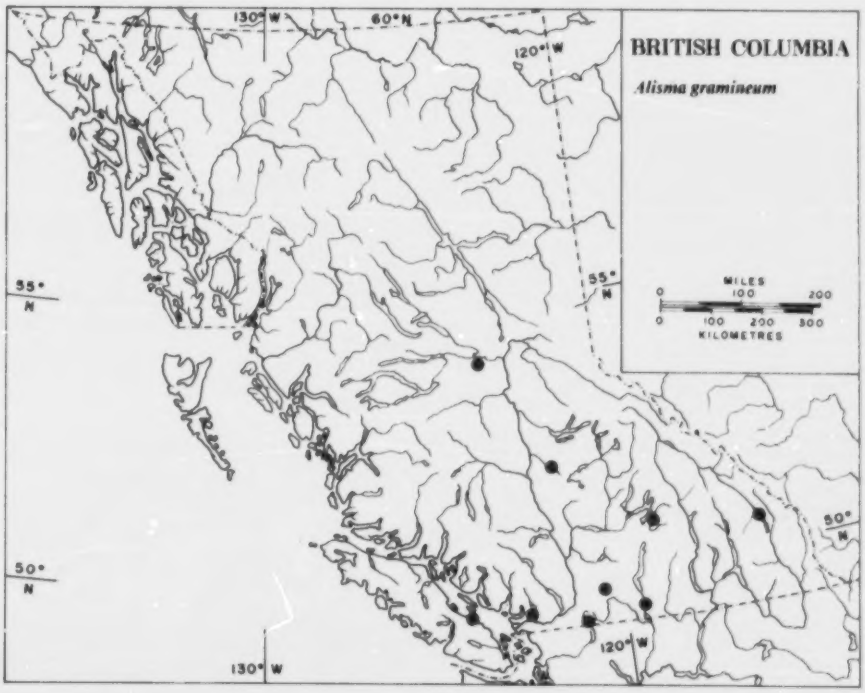
130° W
120° W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60° N
120° W
BRITISH COLUMBIA
Alisma gramineum
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MILES
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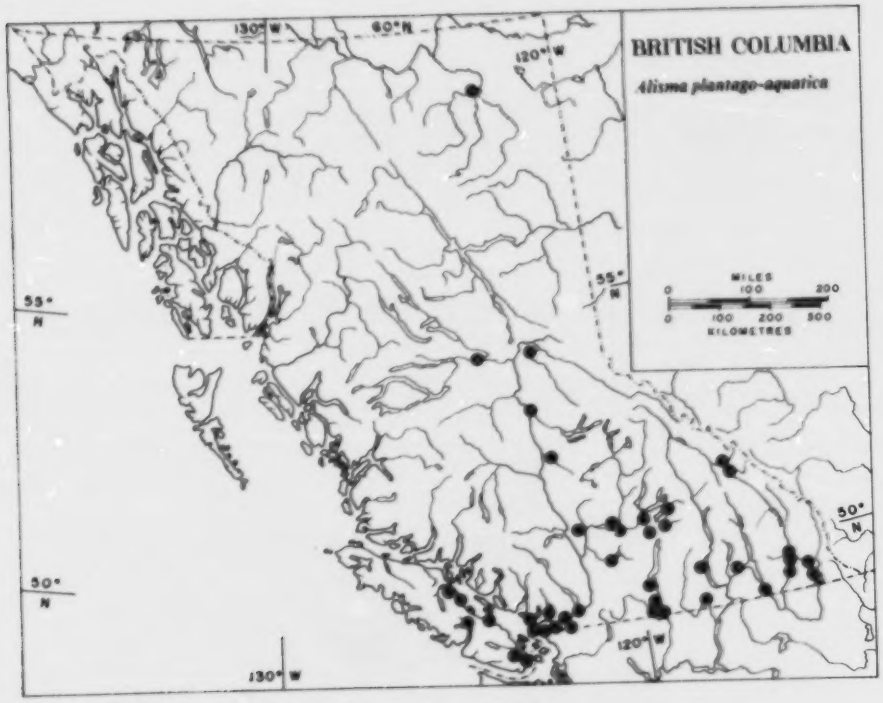
KILOMETRES
50° N
130° W
120° W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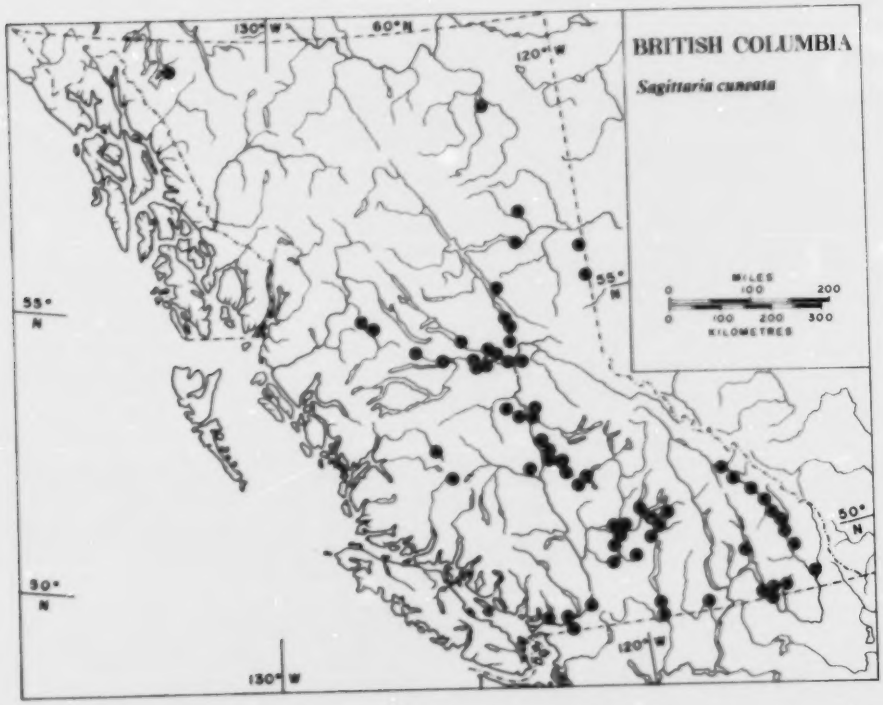
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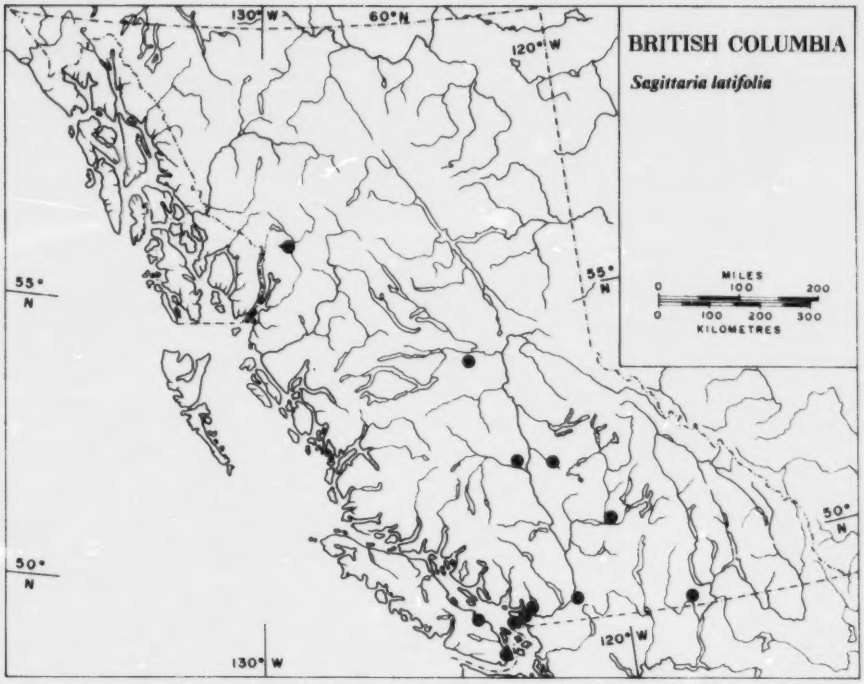
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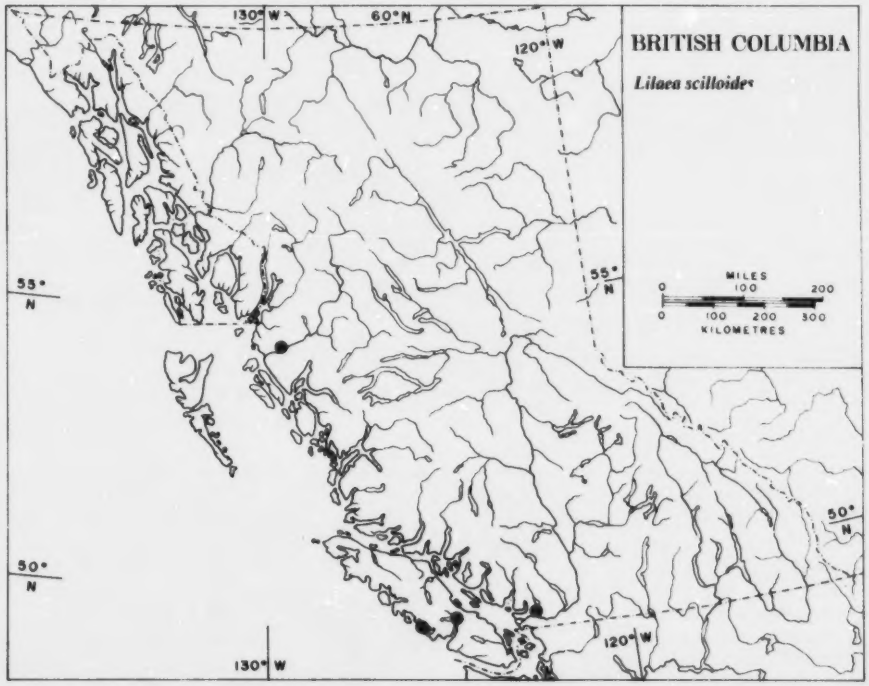
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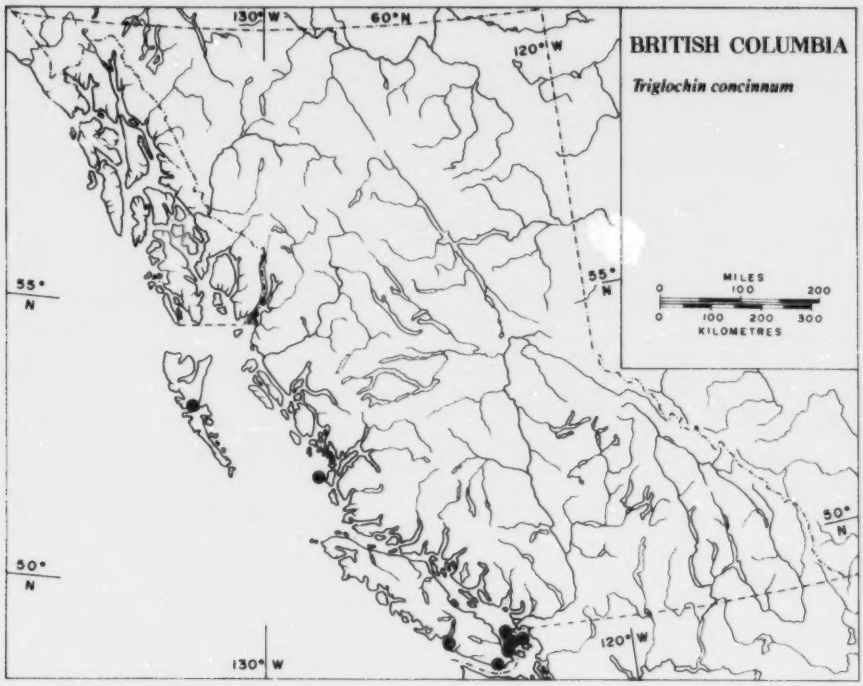
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Triglochin concinnum
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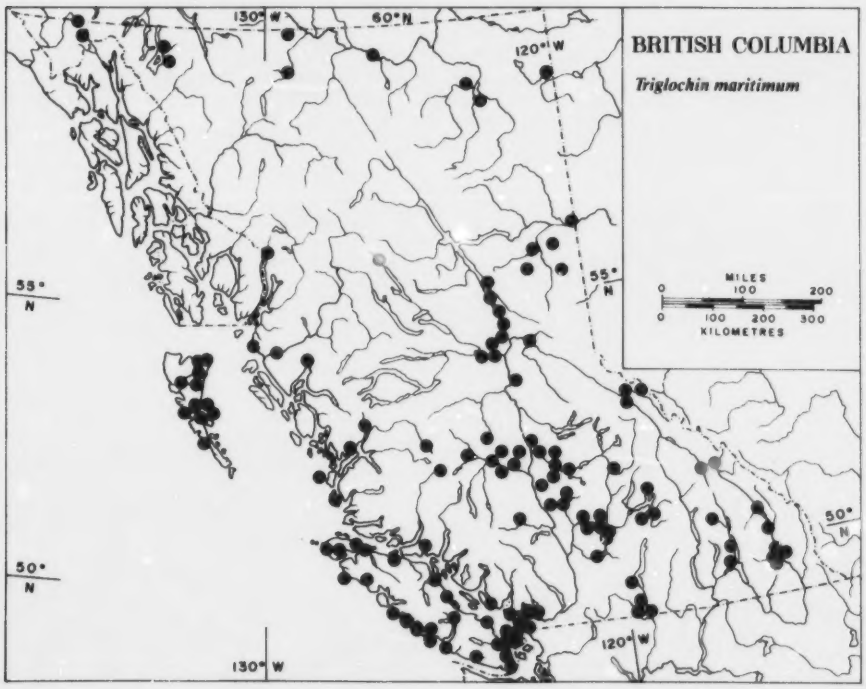
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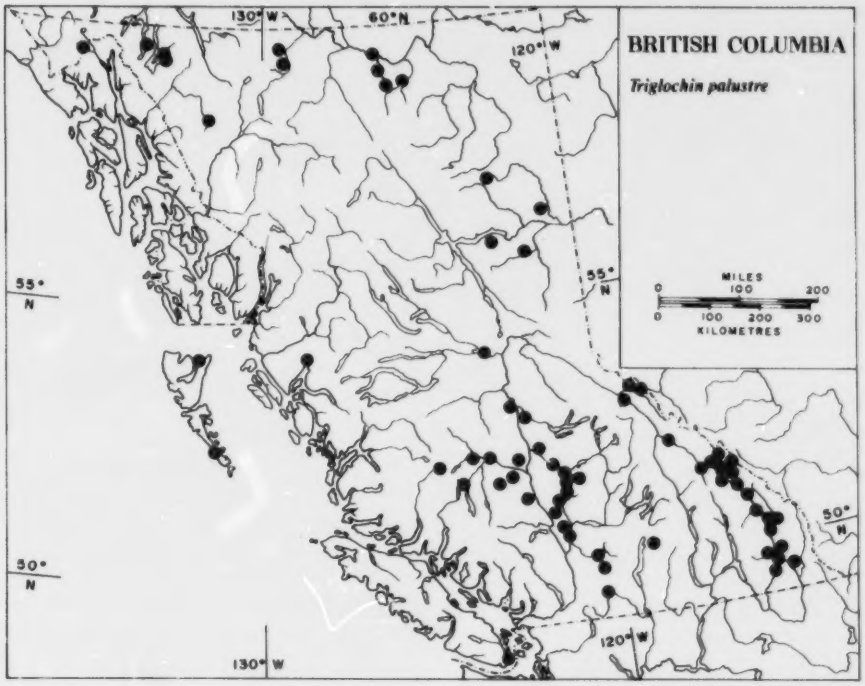
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Triglochin palustre
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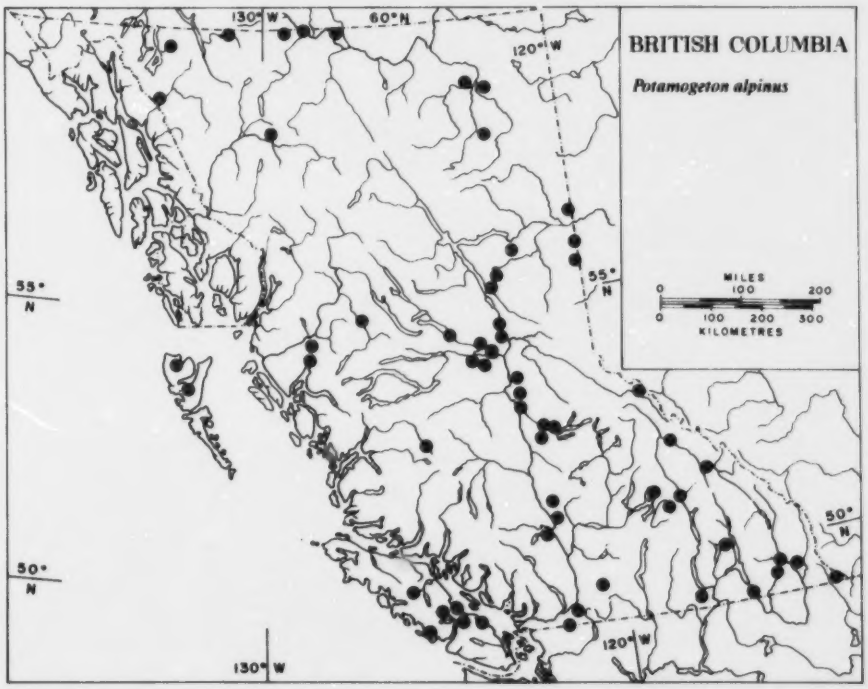
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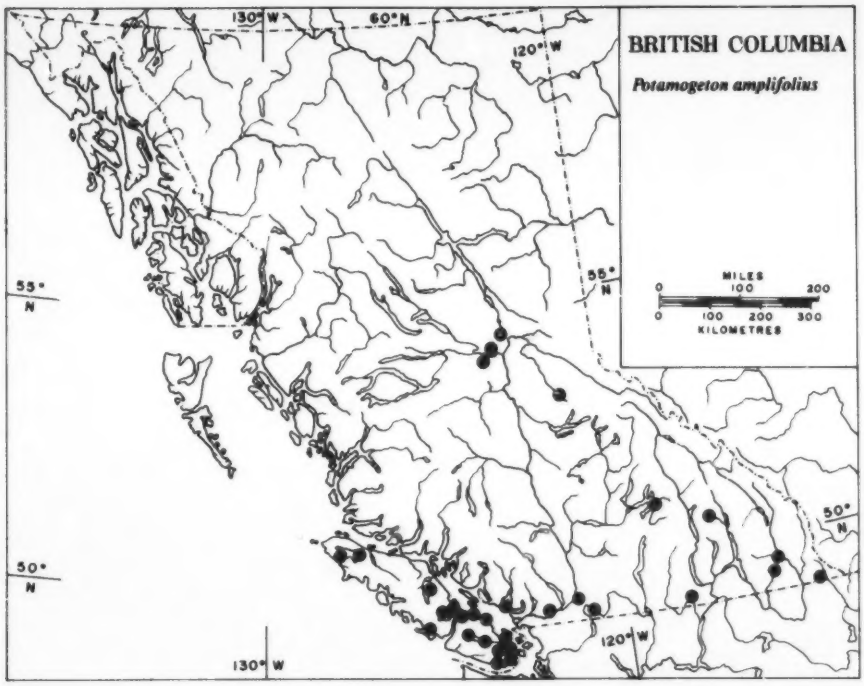
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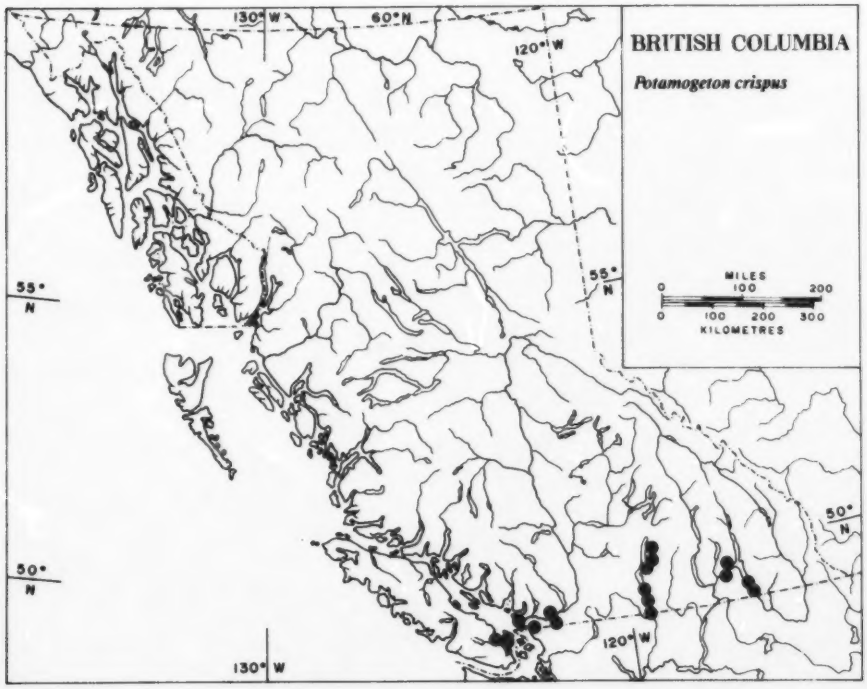
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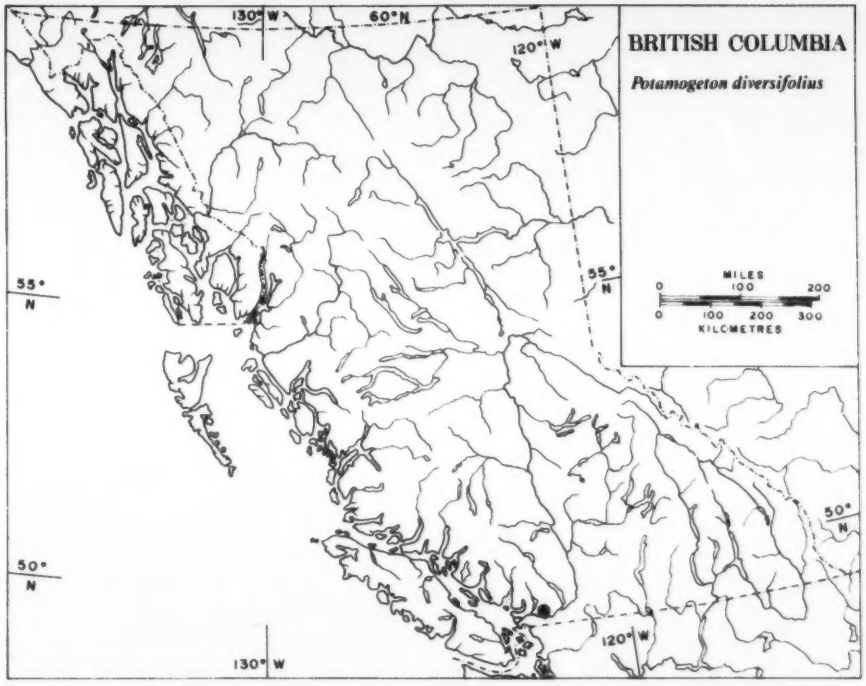
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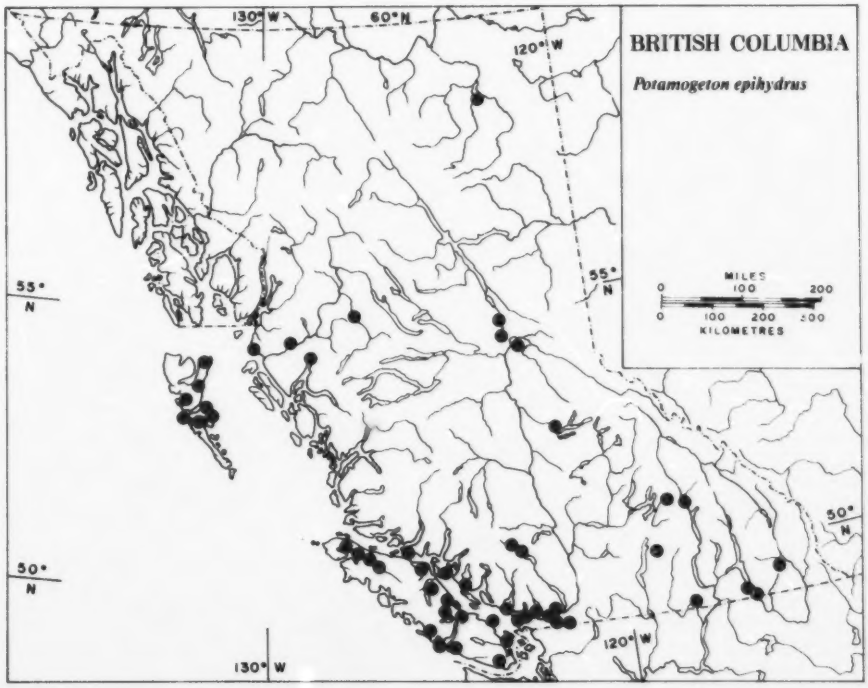
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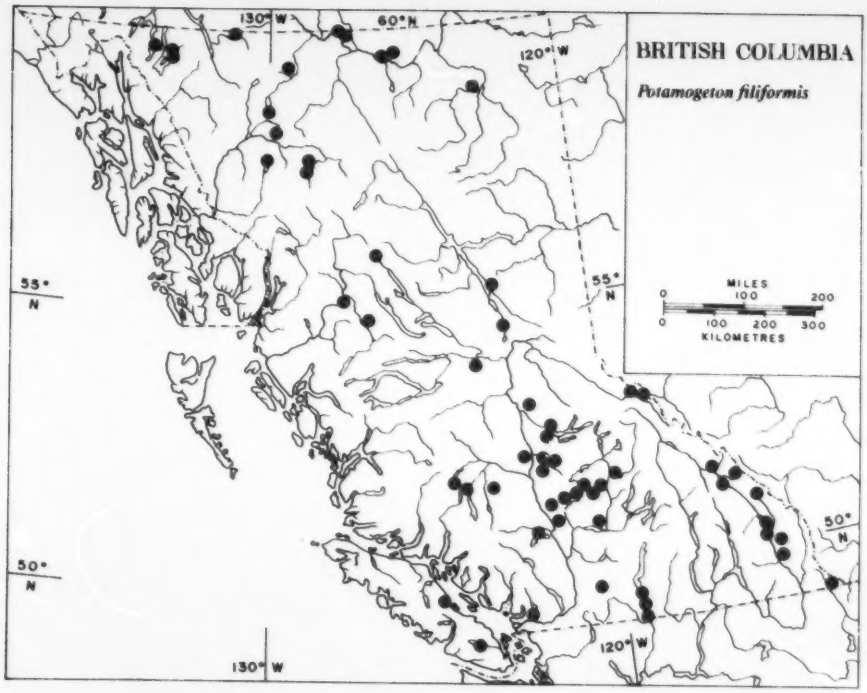
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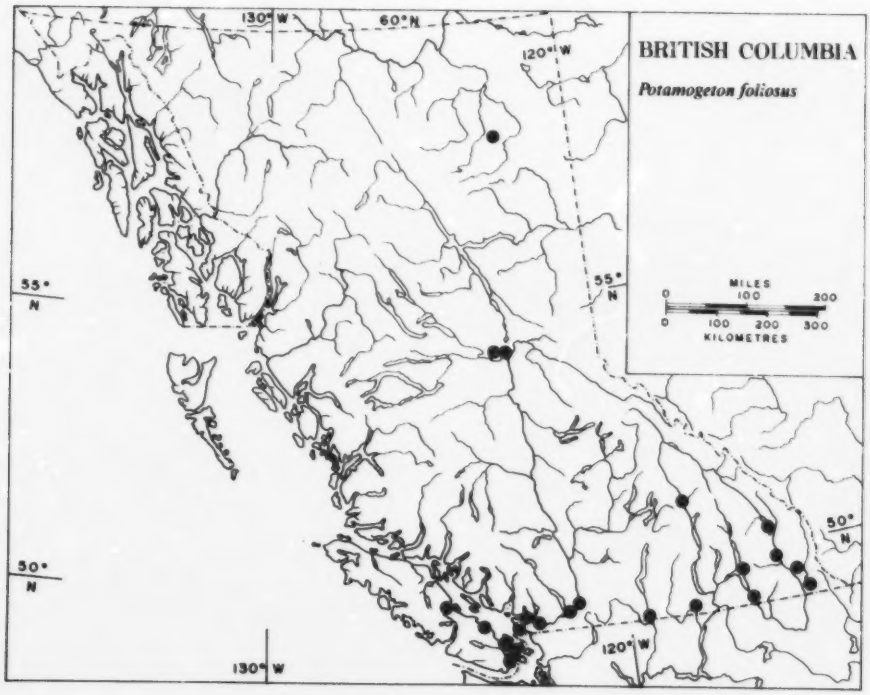
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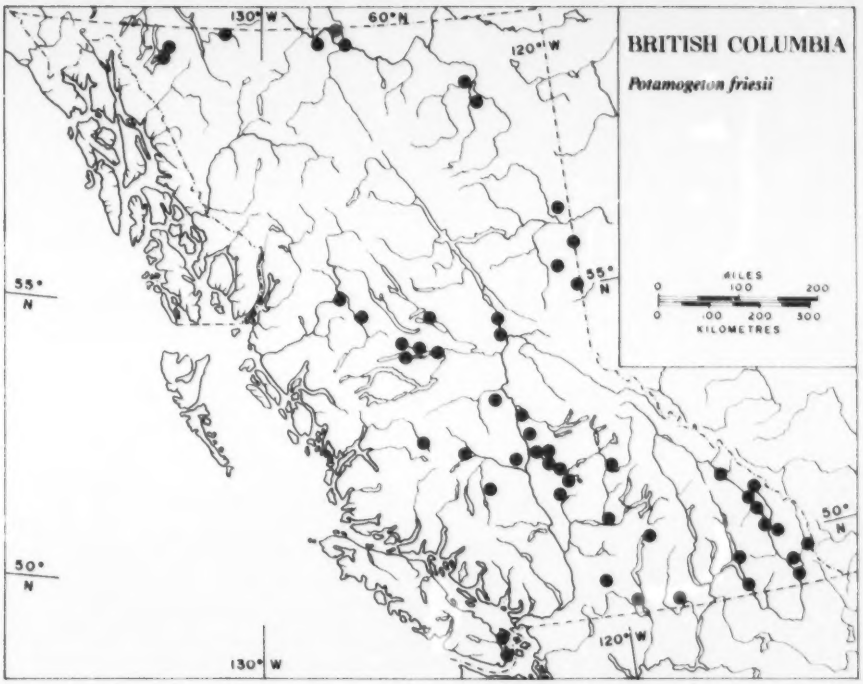
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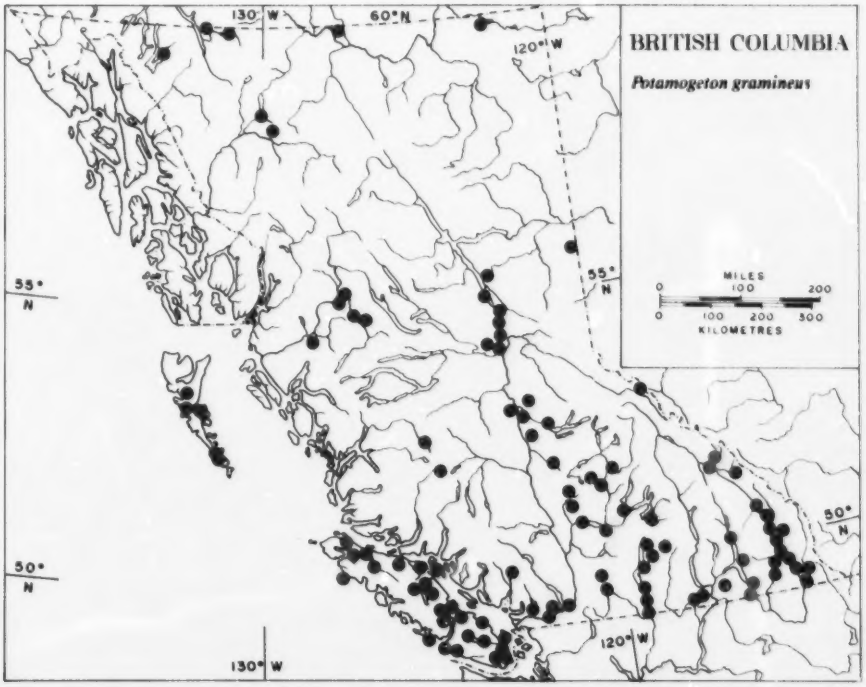
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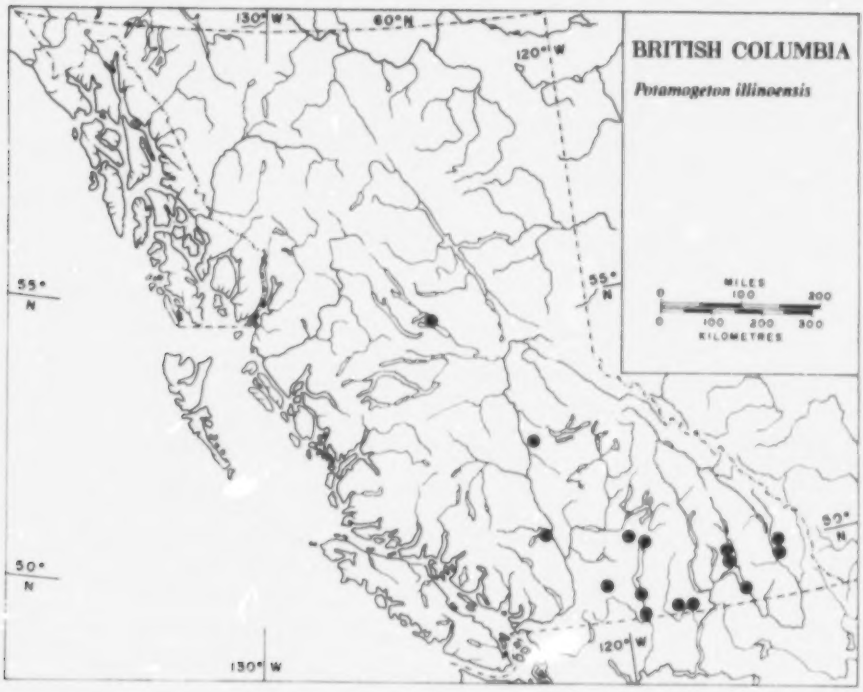
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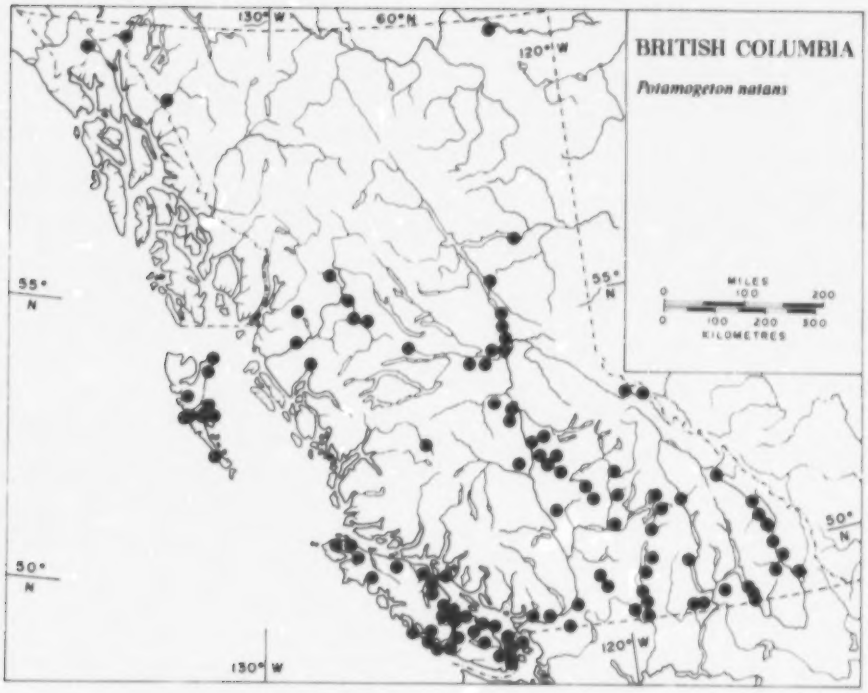
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Potamogeton natans
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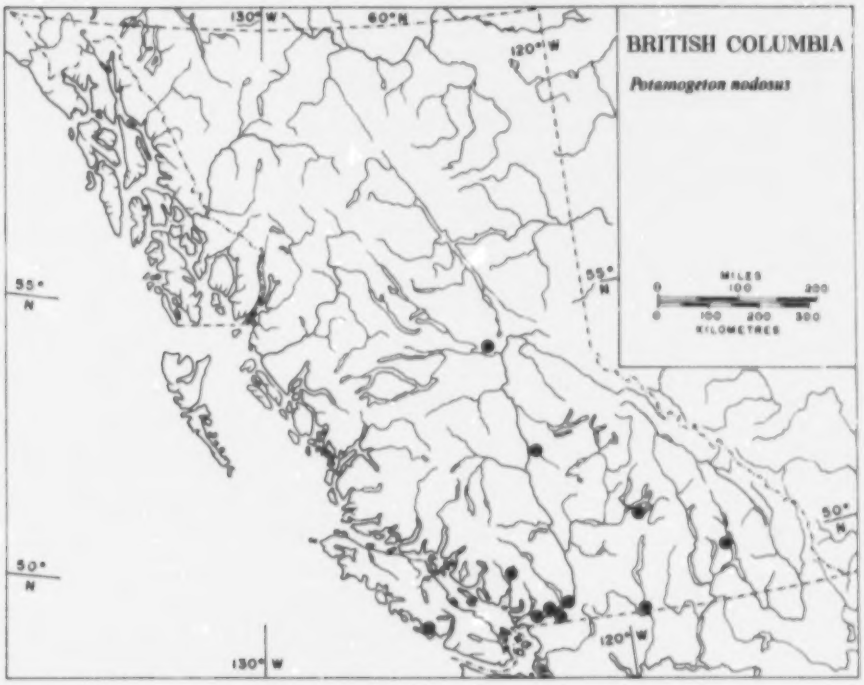
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Potamogeton nodosus
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KILOMETRES
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120° W
55° N
50° N

BRITISH COLUMBIA
Potamogeton oakesianus
MILES
0 100 200
0 100 200 300
KILOMETRES
130° W
60° N
120° W
55° N
50° N

BRITISH COLUMBIA
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MILES
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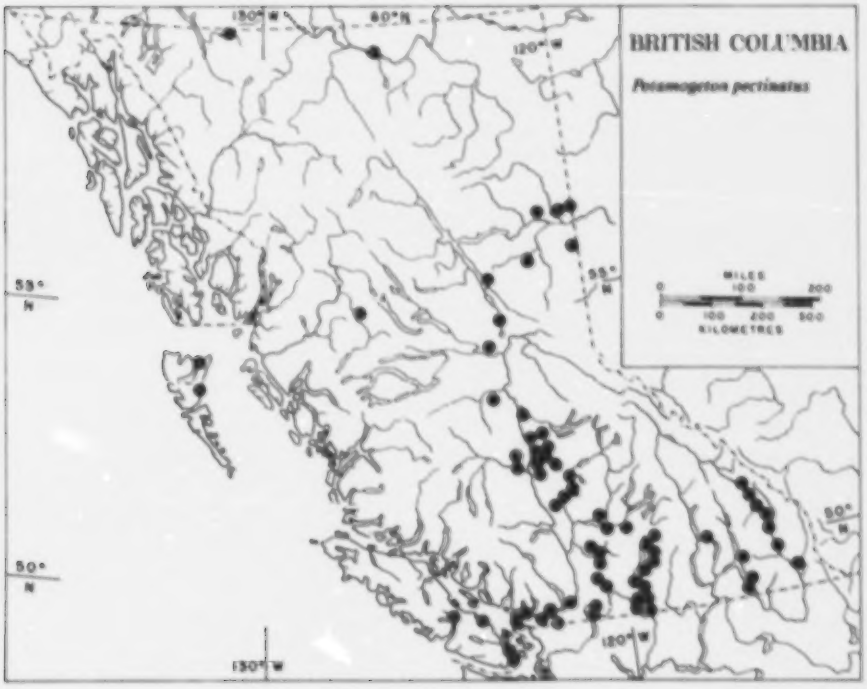
130°W
120°W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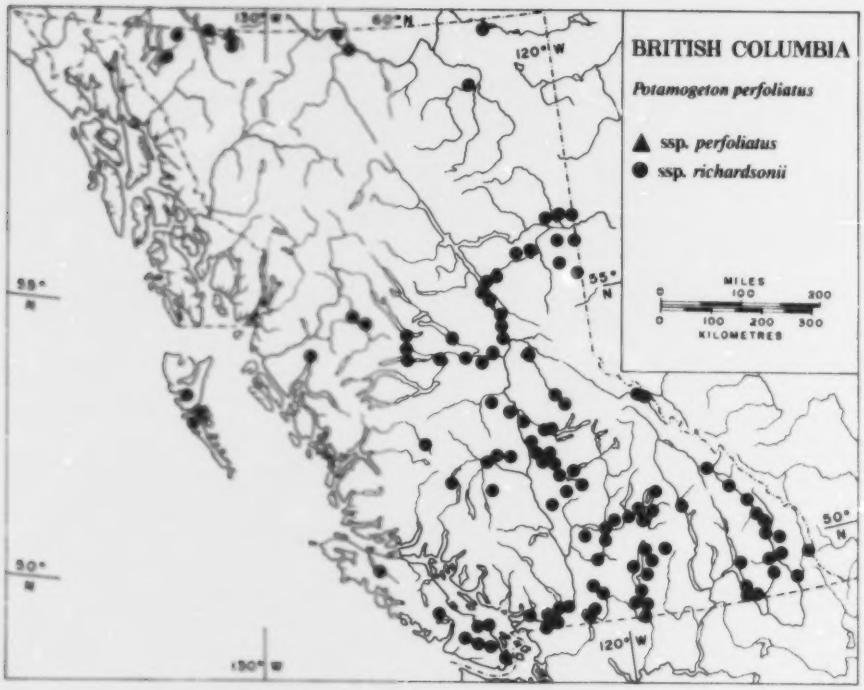
Potamogeton pectinatus
MILES
KILOMETRES
60°N
55°N
50°N
130°W
120°W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Potamogeton perfoliatus
ssp. perfoliatus
ssp. richardsonii
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120° W
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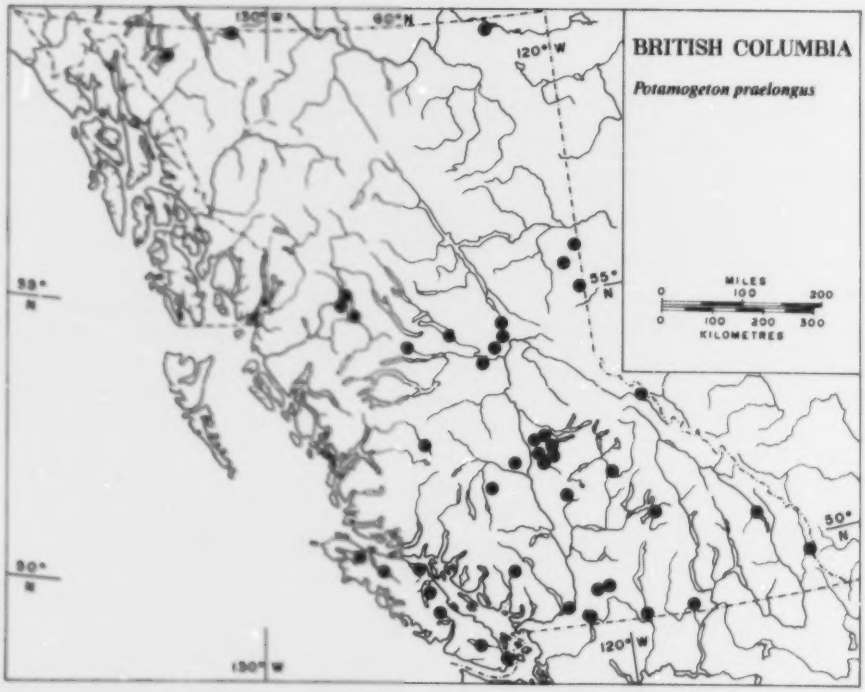
130° W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Potamogeton praelongus
MILES
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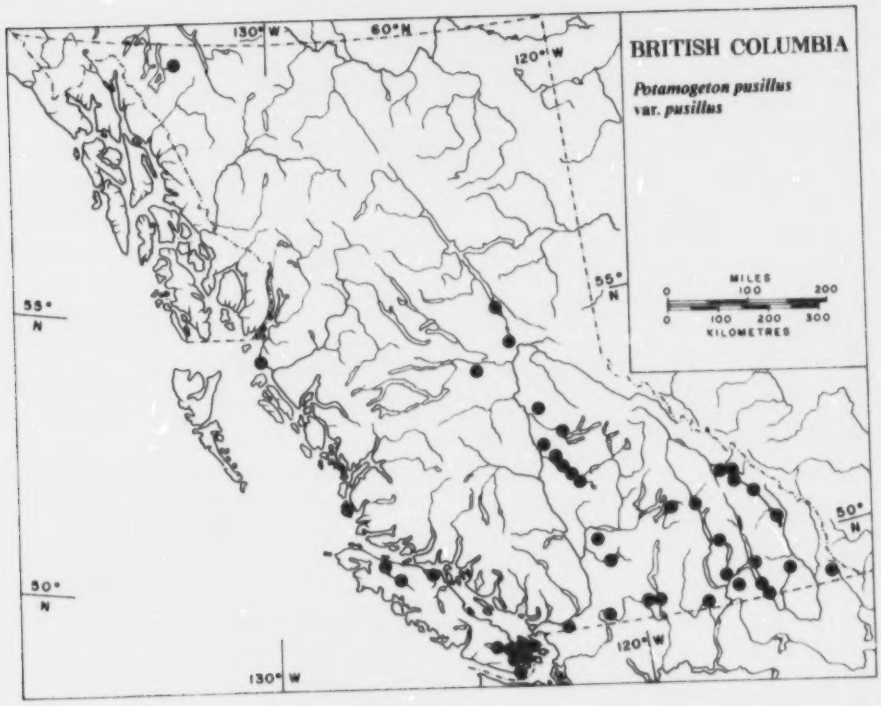
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var. pusillus
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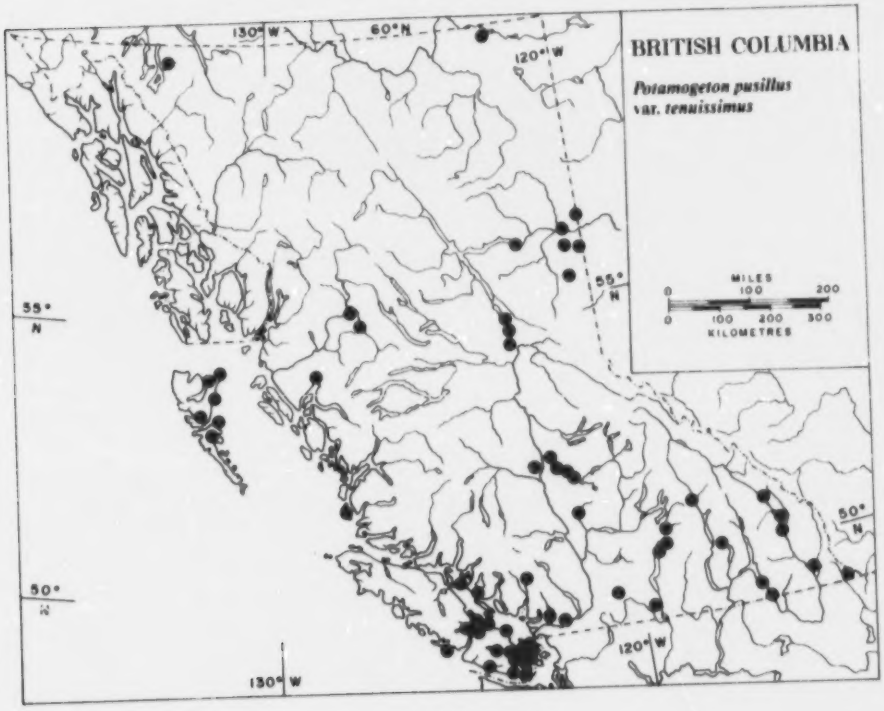
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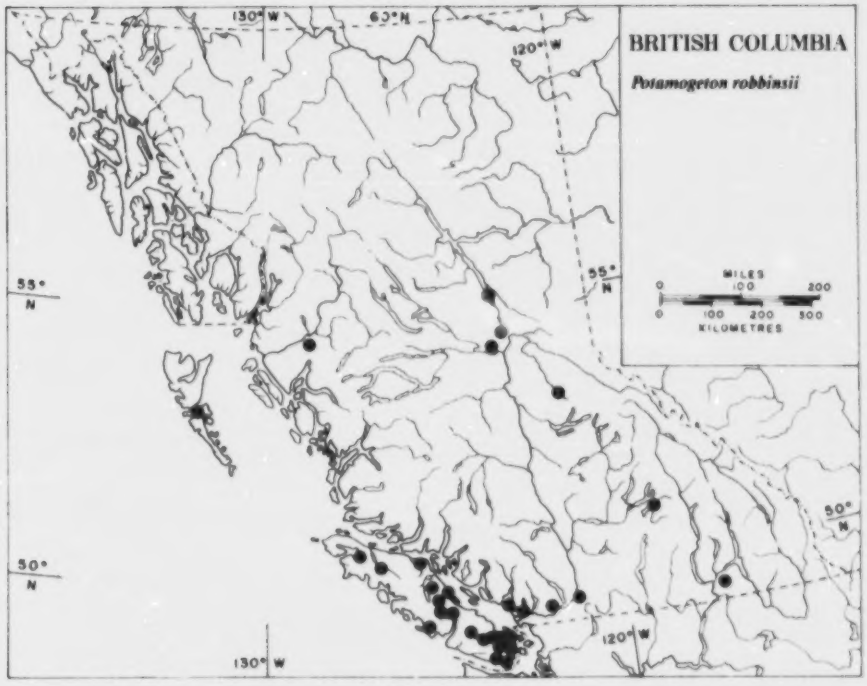
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Potamogeton robbinsii
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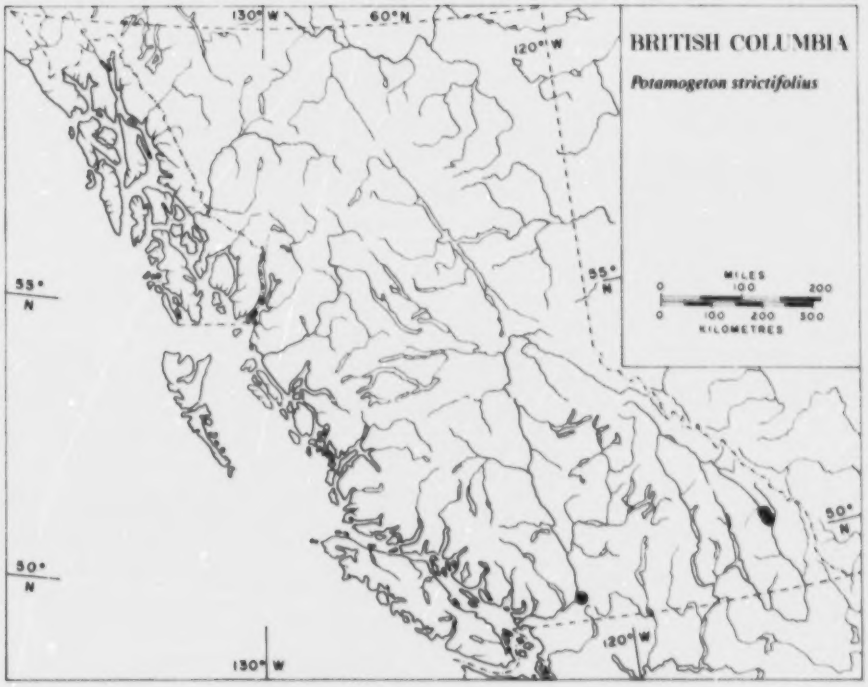
50° N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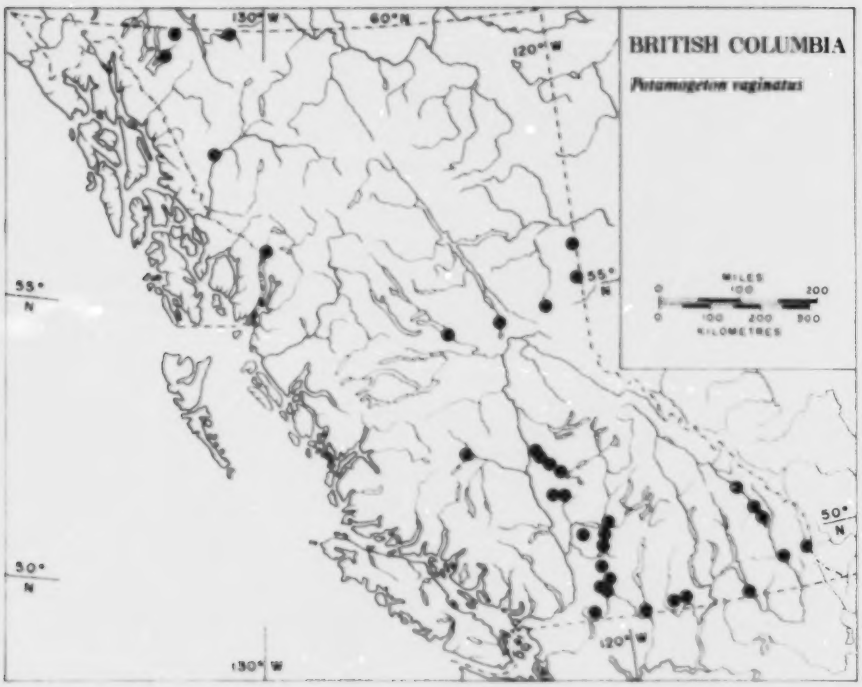
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MILES
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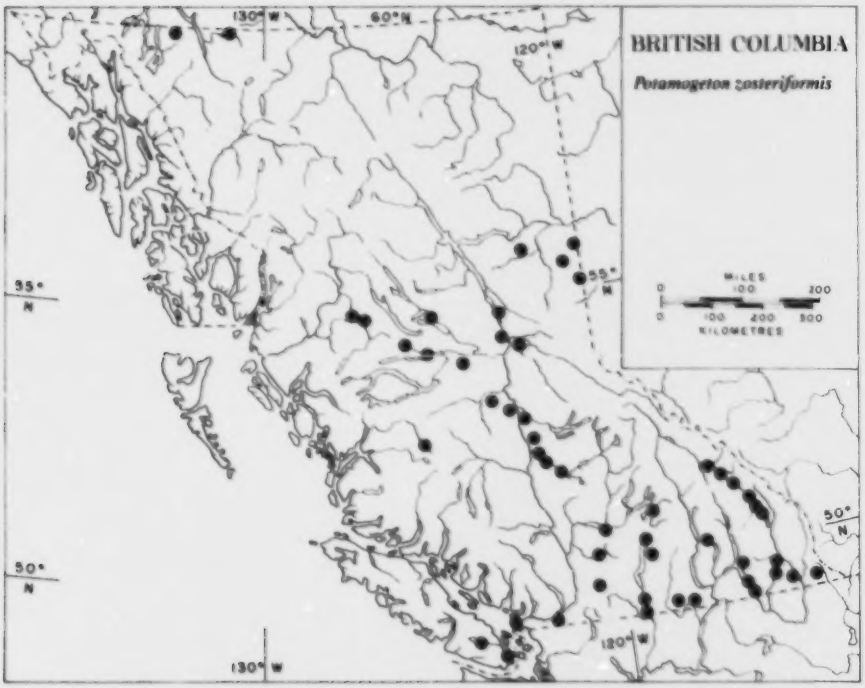
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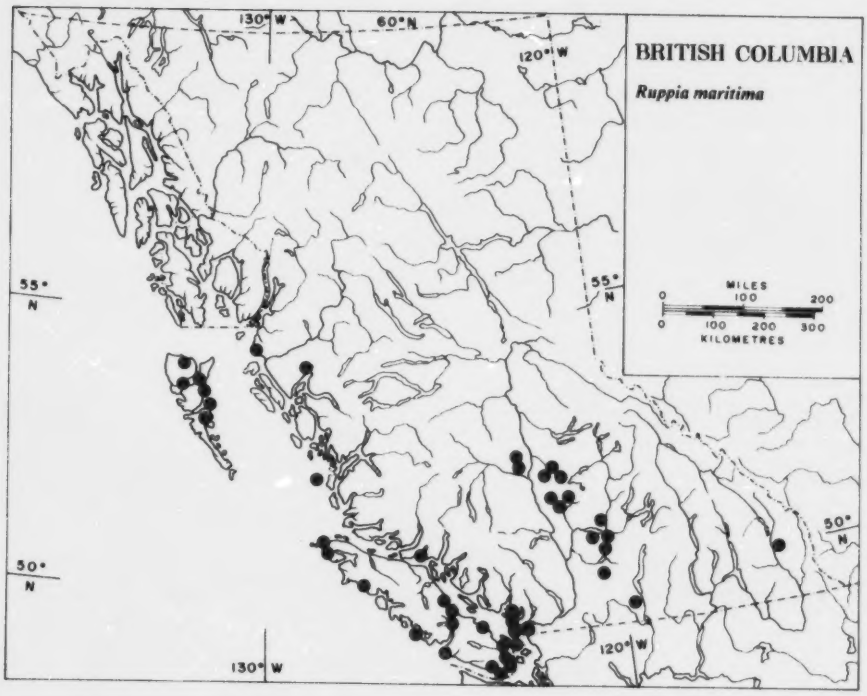
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MILES
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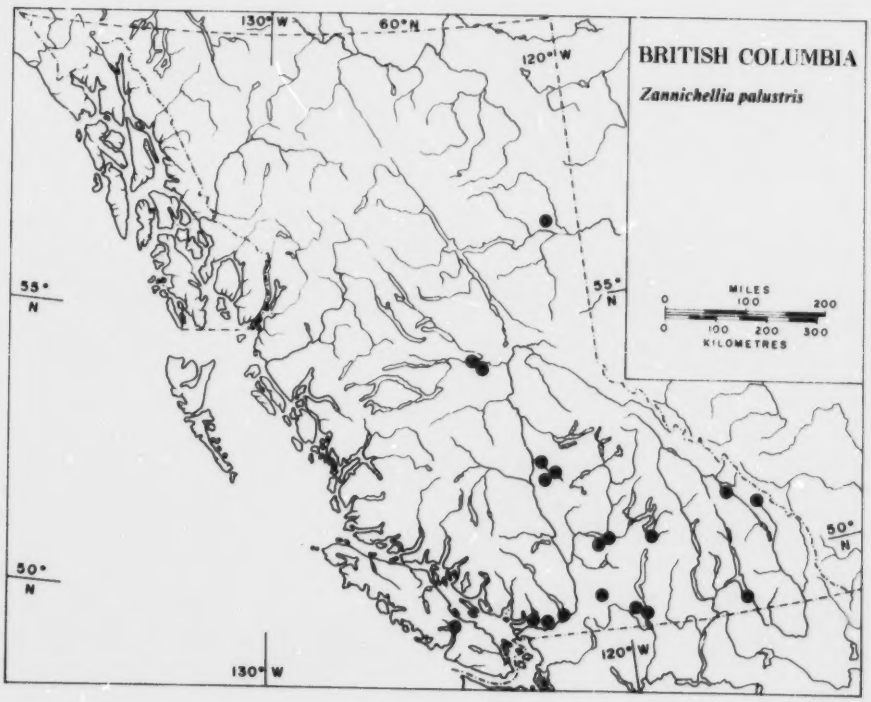
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Zannichellia palustris
130° W
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MILES
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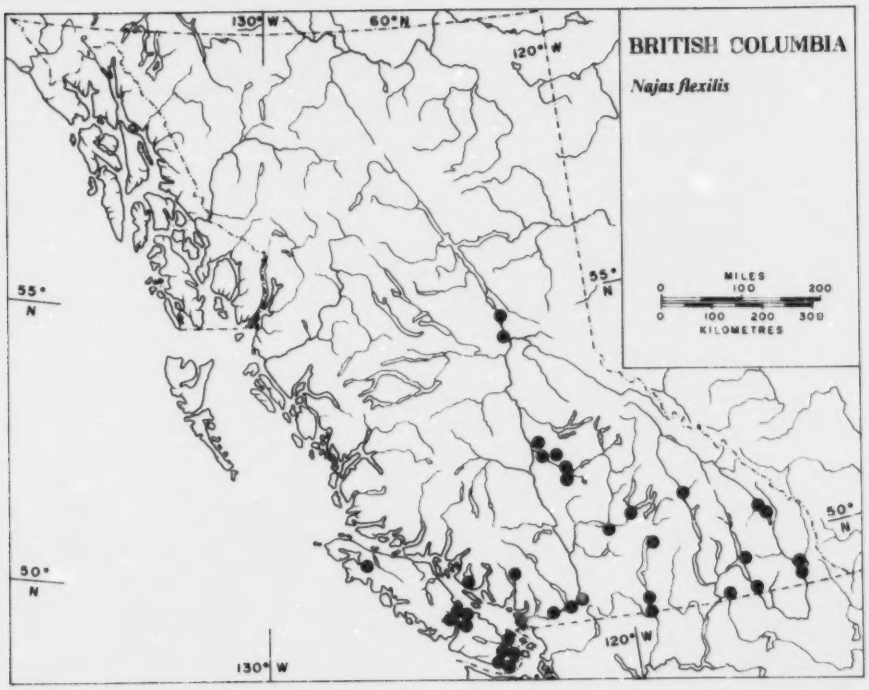
KILOMETRES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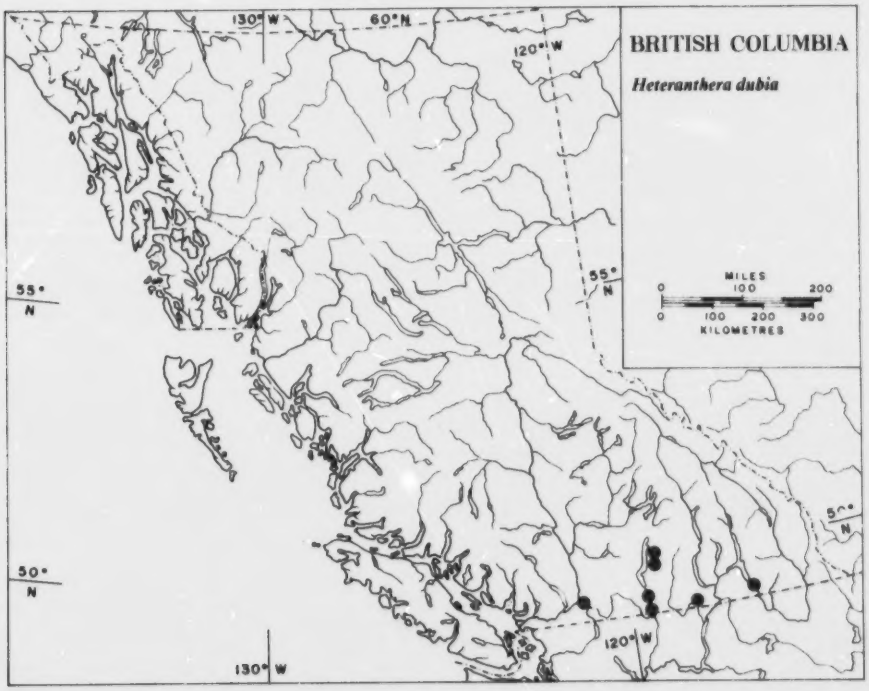
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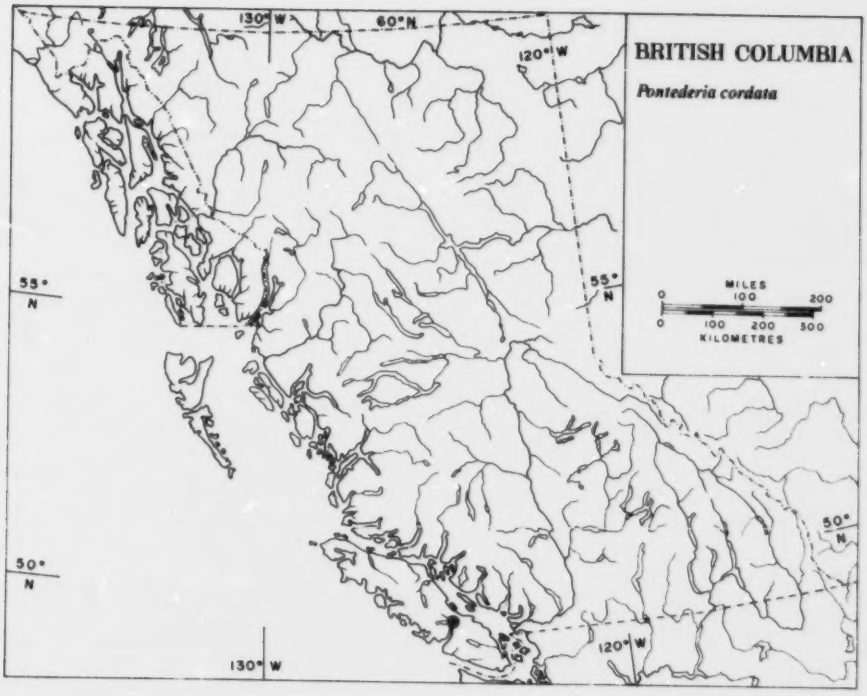
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MILES
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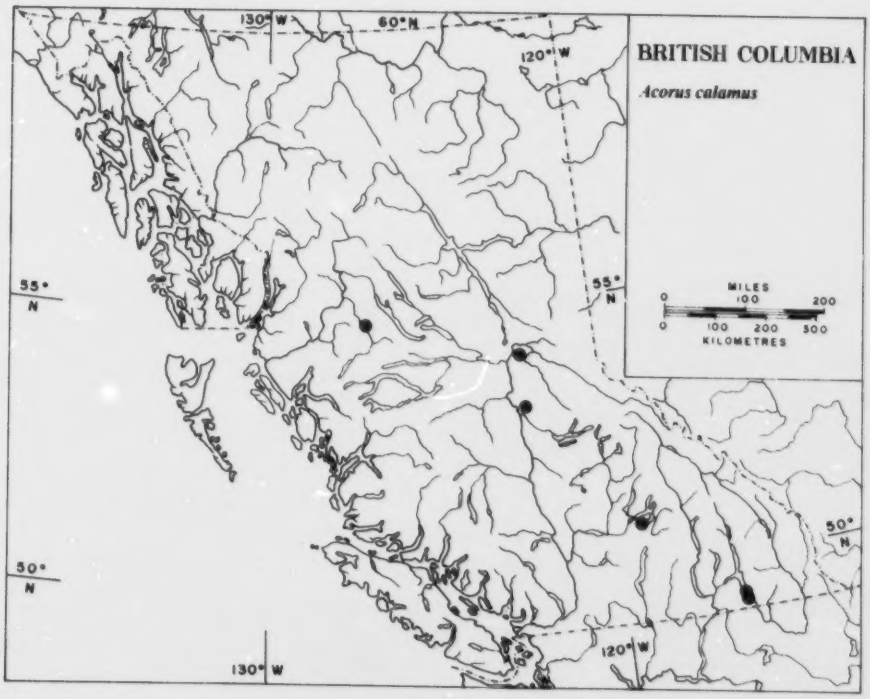
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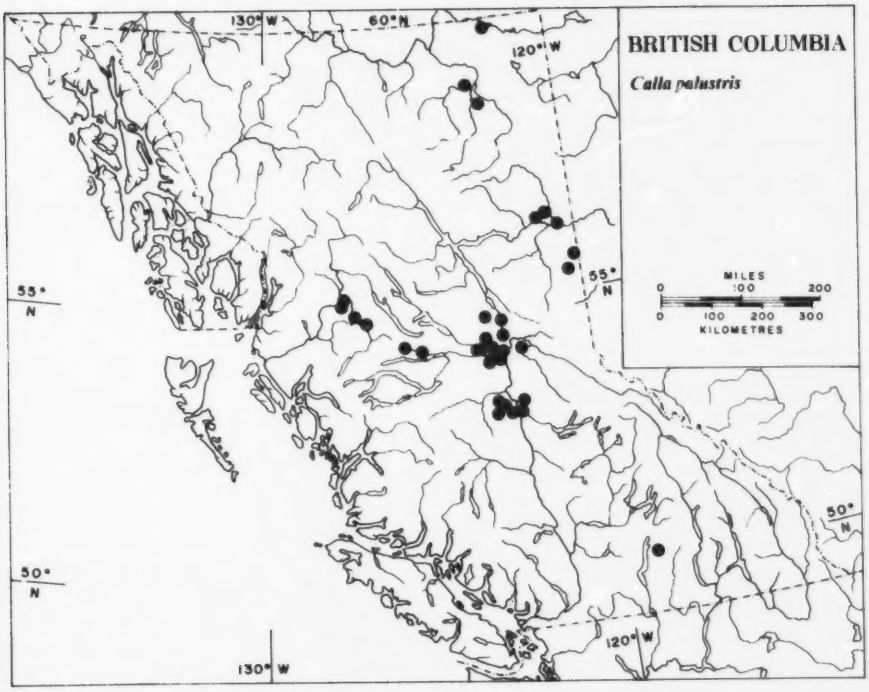
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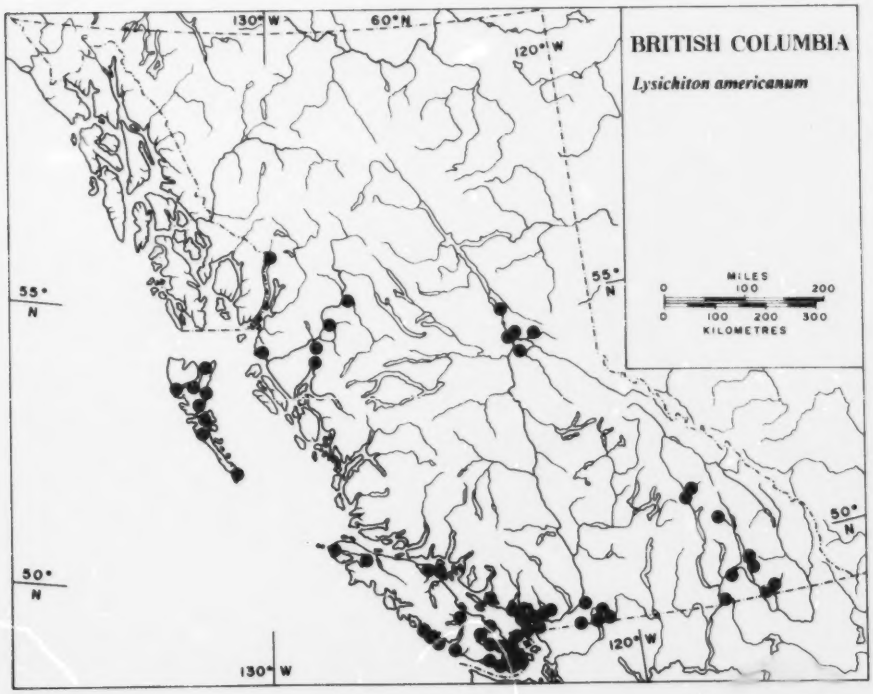
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MILES
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KILOMETRES
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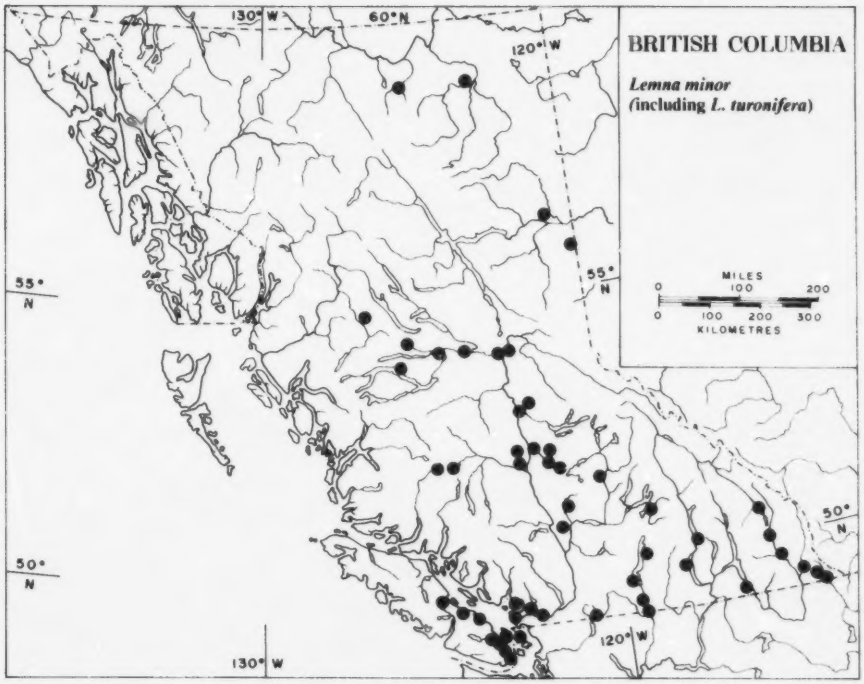
50° N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Lemna minor
(including L. turonifera)
MILES
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KILOMETRES
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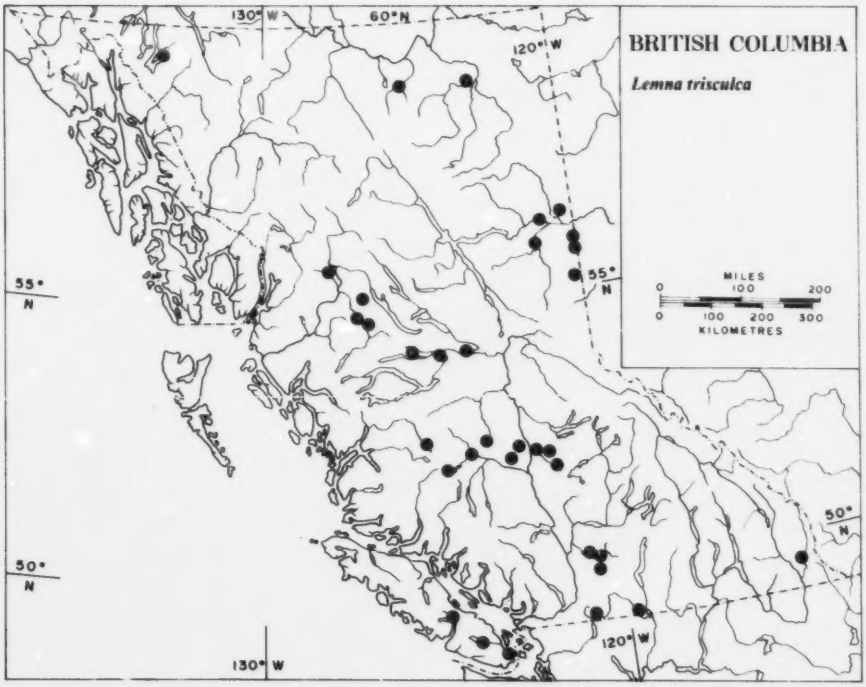
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Lemna trisculca
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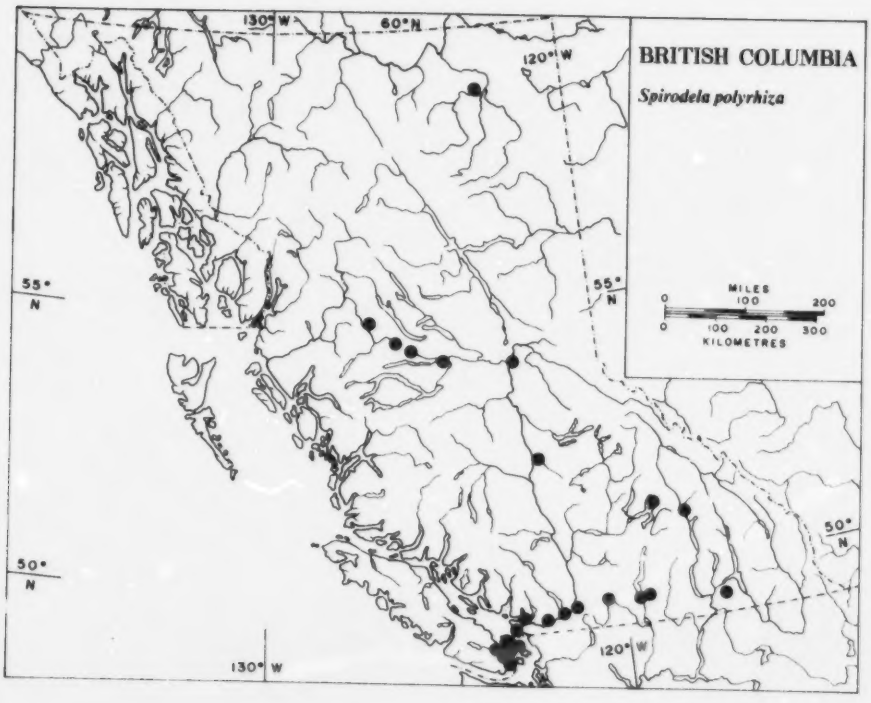
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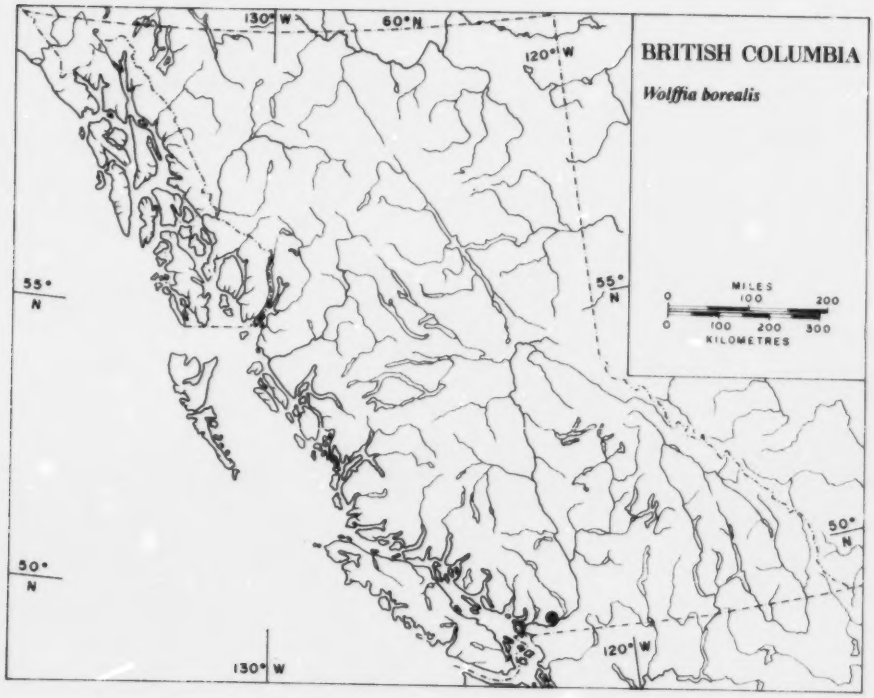
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Wolffia borealis
MILES
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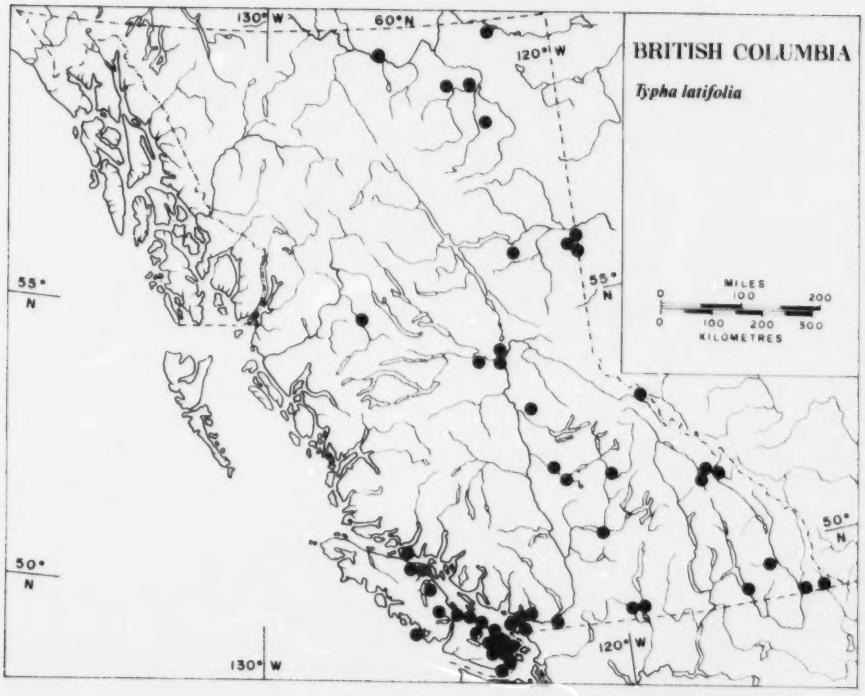
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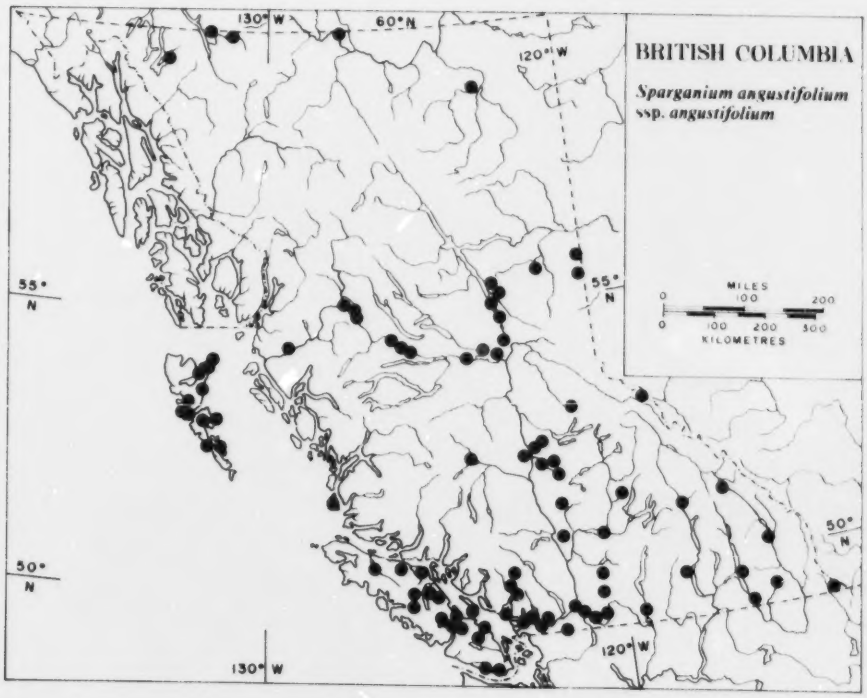
Typha latifolia
130° W
60° N
120° W
55° N
50° N
MILES
0 100 200
0 100 200 300
KILOMETRES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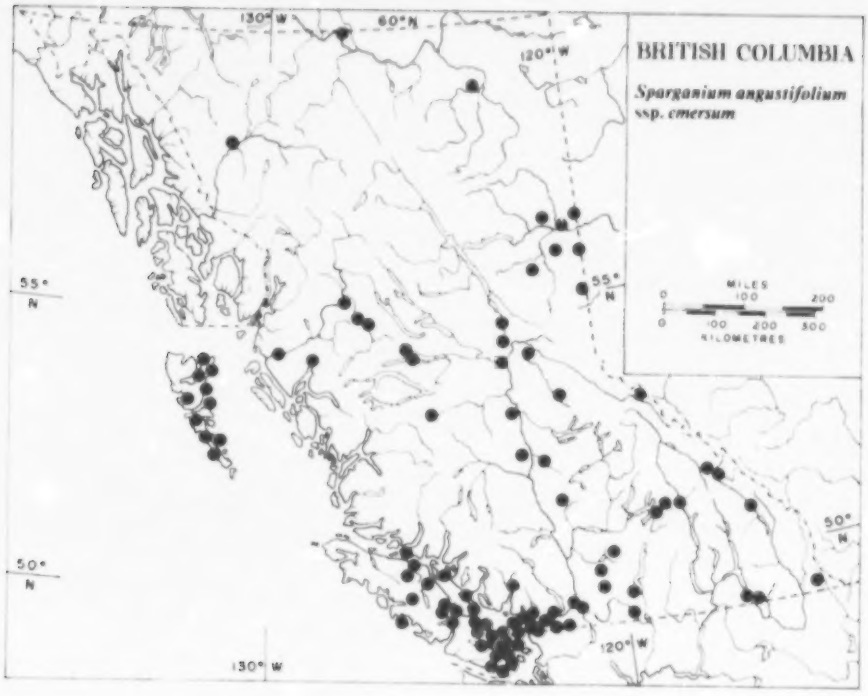
Sparganium angustifolium
ssp. angustifolium
130° W
60° N
120° W
55° N
50° N
MILES
0 100 200
0 100 200 300
KILOMETRES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Sparganium angustifolium
ssp. emersum
MILES
0 100 200
0 100 200 300
KILOMETRES
130° W
60° N
120° W
55° N
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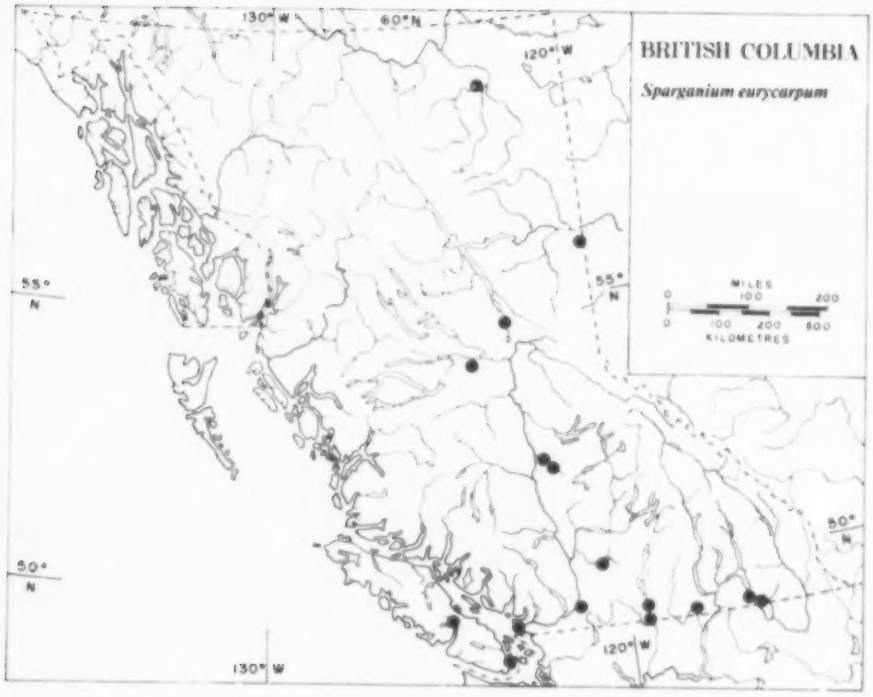
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Sparganium eurycarpum
MILES
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0 100 200 300
KILOMETRES
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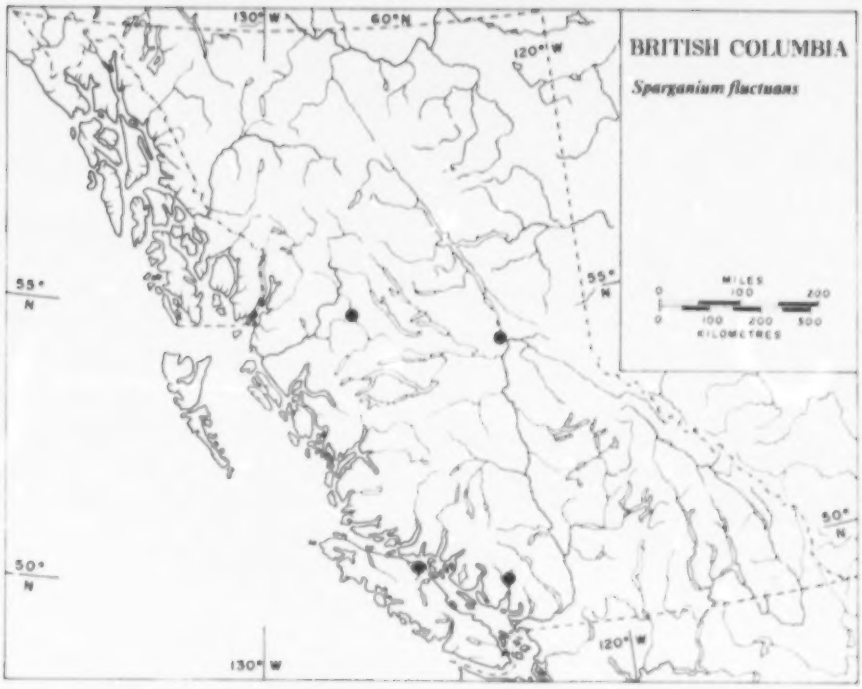
55° N
50° N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130° W
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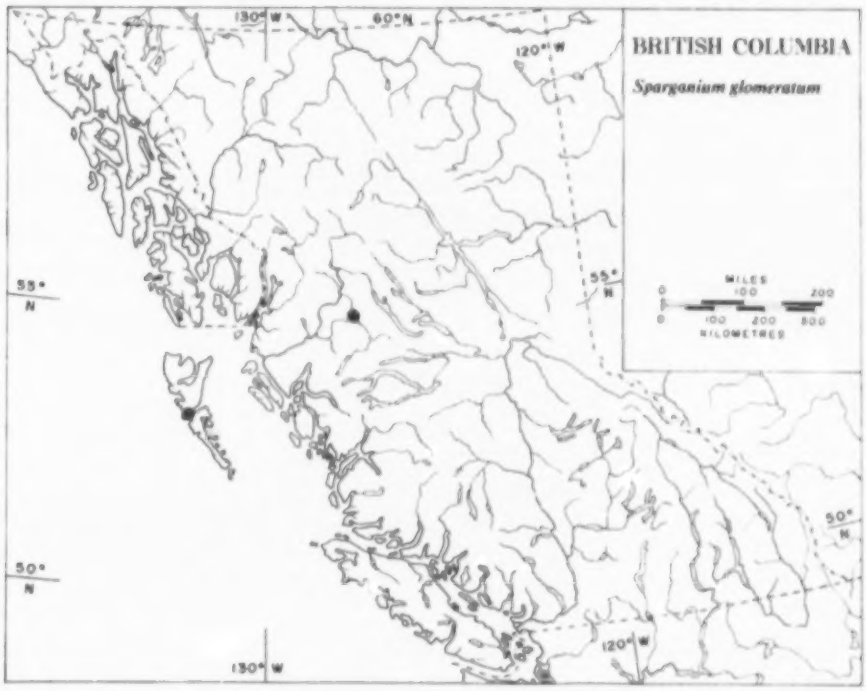
55° N
50° N
MILES
0 100 200
0 100 200 300
KILOMETRES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MILES
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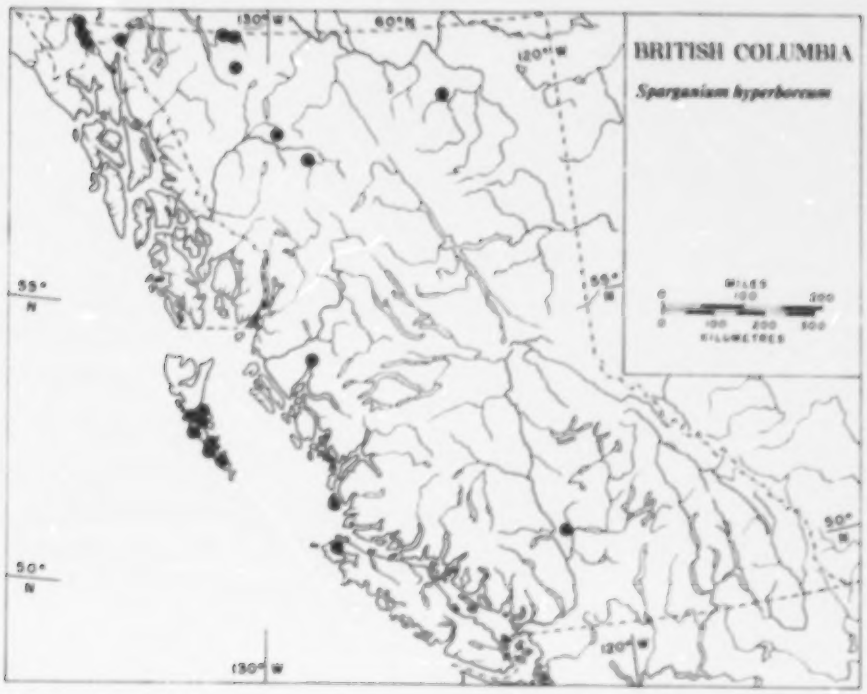
KILOMETRES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Sparganium hyperboreum
MILES
KILOMETRES
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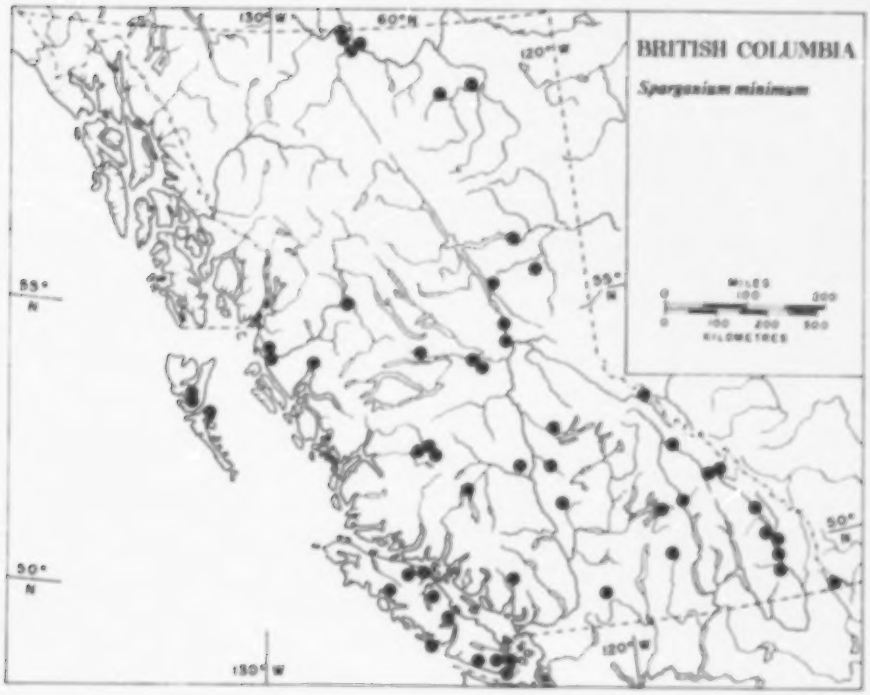
50° N


BRITISH COLUMBIA
Sparganium minimum
MILES
KILOMETRES
130° W
60° N
120° W
55° N
50° N

BIBLIOGRAPHY

In addition to those specifically cited in the text, the following list includes a number of additional references that the author has found heipful in a general way.

ARBER, AGNES. 1920. Water Plants. Cambridge University Press, Cambridge. Reprinted 1963 by J. Cramer, Weinheim.

BOIVIN, BERNARD. 1967. Enumeration Des Plantes Du Canada. Provancheria No. 6, *in* Nat. Can. 93:515–519. Université Laval, Quebec.

CALDER, JAMES A. and ROY L. TAYLOR. 1968. Flora Of The Queen Charlotte Islands: Monograph #4, Part 1. Research Branch, Canada Dept. Agr., Ottawa.

CESKA, ADOLF and OLDRISKA CESKA. 1980. Additions To The Flora Of British Columbia. Can. Field-Nat. 94(1):69–74.

CHARLTON, W. A. 1973. Studies In The Alismataceae, II: Inflorescences Of Alismataceae. Can. J. Bot. 51:775–789.

_____ and A. AHMED. 1973. Studies In The Alismataceae, IV: Developmental Morphology Of *Ranalisma humile* And Comparisons With Two Members Of The Butomaceae, *Hydrocleis nymphoides* And *Butomus umbellatus*. Can. J. Bot. 51:899–910.

CLAPHAM, A. R., T. G. TUTIN and E. F. WARBURG. 1958. Flora Of The British Isles. Cambridge University Press, Cambridge.

COOK, C. D. K. 1968. Phenotypic Plasticity With Particular Reference To Three Amphibious Plant Species. *In* Heywood, V. E., ed. Modern Methods In Plant Taxonomy. Ch. 8:97–111. Academic Press, London.

_____, BERNARD J. GUT, E. MARTYN RIX, JAKOB SCHNELLER and MARTA SEITZ. 1974. Water Plants Of The World. Dr. W. Junk b.v., The Hague.

CRONQUIST, ARTHUR. 1968. The Evolution And Classification Of Flowering Plants. Houghton Mifflin, Boston.

DACEY, J. W. H. 1980. Internal Winds In Water Lilies: An Adaptation For Life In Anaerobic Sediments. Science 210:1017–1019.

DALE, H. M. and T. J. GILLESPIE. 1977. The Influence Of Submerged Aquatic Plants On Temperate Gradients In Shallow Water Bodies. Can. J. Bot. 55:2216–2225.

DANDY, J. E. 1980. Potamogeton. *In* Tutin, T. G., V. H. Heywood, N. A. Burges, D. M. Moore, D. H. Valentine, S. M. Walters and D. A. Webb, Flora Europaea. Volume 5. Cambridge University Press, London.

_____ and G. TAYLOR. 1938–1942. Studies Of British Potamogetons: I–XVIII. Journ. Bot., Vols. 76–80. Linnaean Society, London.

DAUBS, EDWIN HORACE. 1965. A Monograph Of Lemnaceae. Illinois Biological Monographs 34. University of Illinois Press, Urbana, Illinois.

DEN HARTOG, C. 1979. The Sea-Grasses Of The World. North Holland, Amsterdam.

DORE, WILLIAM G. 1957. *Wolffia* In Canada. Can. Field-Nat. 71:10–16.

FASSETT, NORMAN C. 1940. A Manual Of Aquatic Plants. McGraw-Hill, New York.

FERNALD, M. L. 1921. Expedition To Nova Scotia. Rhodora 23:184–195.

FERNALD, M. L. 1950. ed. Gray's Manual Of Botany. (8th ed.) American Book Co., New York.

_____ and K. M. WIEGAND. 1914. *Ruppia* In North America. Rhodora 16:119–127 and pl. 110.

HARMS, VERNON L. 1973. Taxonomic Studies Of North American *Sparganium:* 1. *S. hyperboreum* And *S. minimum*. Can. J. Bot. 51:1629–1641.

HARRISON, PAUL GARTH. 1976. *Zostera japonica* (Aschers. and Graebn.) In British Columbia, Canada. Syesis 9:359–360.

HAYNES, ROBERT R. 1974. A Revision Of North American *Potamogeton* Subsection *Pusilli* (Potamogetonaceae). Rhodora 76:564–649.

HITCHCOCK, C. LEO. 1969. All aquatic families of Monocotyledons. *In* Hitchcock, C. Leo, Arthur Cronquist, Marion Ownbey and J. W. Thompson, Vascular Plants Of The Pacific Northwest. Part 1. University of Washington Press, Seattle.

HULTEN, ERIC. 1968. Flora Of Alaska And Neighboring Territories. Stanford University Press, Stanford.

HUTCHINSON, J. 1959. The Families Of Flowering Plants. Ed. 2., 2 vols. Oxford University Press London.

LANDOLT, ELIAS. 1975. Morphological Differentiation And Geographical Distribution Of The *Lemna gibba-Lemna minor* Group. Aquatic Botany 1(4):345–363. Elsevier, Amsterdam.

_____ (ed). 1980. Biosystematische Untersuchungen in der Familie der Wasserlinsen (Lemnaceae). Veröff. Geobot. Inst. Eth. Siftung Rübel, Zürich: heft. 70.

LINNAEUS, CARL. 1753. Species Plantarum: Edition 1. Facsimile Reprint, 1957, Ray Society, London.

MUENSCHER, WALTER CONRAD. 1944. Aquatic Plants Of The United States. Comstock, Ithaca, N.Y.

OGDEN, E. C. 1943. The Broad-Leaved Species Of *Potamogeton* Of North America North Of Mexico. Rhodora 45:57–105, 119–163, 171–214.

OGDEN, EUGENE C. 1953. Key To The North American Species Of *Potamogeton*. New York State Museum: circular 31. Albany, N.Y.

PHILLIPS, RONALD C. 1979. Ecological Notes On *Phyllospadix* (Potamogetonaceae) In The Northeast Pacific. Aqu. Bot. 6:159–170. Elsevier, Amsterdam.

POSLUSZNY, U. and R. SATTLER. April, 1976a. Floral Development of *Zannichellia palustris*. Can. J. Bot. 54(8):651–662.

_____ and _____ . May, 1976b. Floral Development Of *Najas flexilis*. Can. J. Bot. 54(10):1140–1151.

REVEAL, JAMES L. 1970. *Sparganium simplex* Huds., A Superfluous Name. Taxon 19:796–797.

ROBBINS, J. W. 1867. *Potamogeton; in* Gray, Manual Of The Botany Of The Northern United States. Ivison, Phinney, Blakeman, New York.

SCOGGAN, H. J. 1978. The Flora Of Canada: Part 2. Publications in Botany 7(2), National Museum of Natural Sciences, Ottawa.

SCULTHORPE, C. D. 1967. The Biology Of Aquatic Vascular Plants. Edward Arnold, London.

SETCHELL, WILLIAM A. 1946. The Genus *Ruppia* L. Proceedings of the California Academy of Sciences 25(18):469–478.

SINGH, V. and R. SATTLER. 1972. Floral Development Of *Alisma triviale*. Can. J. Bot. 50:619–627.

_____ and _____ . 1973. Nonspiral Androecium And Gynoecium Of *Sagittaria latifolia*. Can. J. Bot. 51:1093–1095.

_____ and _____ . 1974. Floral Development Of *Botumus umbellatus*. Can. J. Bot. 52:223–230.

SPENCE, D. H. N. and H. M. DALE. 1978. Variations In The Shallow Water Form Of *Potamogeton richardsonii* Induced By Some Environmental Factors. Freshwater Biology 8:251–268.

STEWARD, ALBERT N., LA REA J. DENNIS and HELEN M. GILKEY. 1963. Aquatic Plants Of The Pacific Northwest. Oregon State University Press, Corvallis.

STUCKEY, RONALD L., JOHN R. WEHRMEISTER and ROBERT J. BARTOLETTE. 1978. Submersed Aquatic Vascular Plants In Ice-covered Ponds Of Central Ohio. Rhodora 80:575–580.

SVEDELIUS, NILS. 1932. On The Different Types Of Pollination In *Vallisneria spiralis* L. and *Vallisneria americana*. Michx. Svensk Botanisk Tidskrift 26,H:1–12.

TAKHTAJAN, AMEN. 1961. Flowering Plants: Origin And Dispersal. English translation by C. Jeffrey, 1969. Oliver and Boyd, Edinburgh.

TAYLOR, ROY L. and BRUCE MACBRYDE. 1977. Vascular Plants Of British Columbia. University of British Columbia Press, Vancouver.

THORNE, ROBERT F. 1976. A Phylogenitic Classification Of The Angiospermae. Evolutionary Biology 9:35–106. Plenum, New York.

WELSH, STANLEY L. 1974. Anderson's Flora Of Alaska And Adjacent Parts Of Canada. Brigham Young University Press, Provo.

YUZEPCHUK, S. V. 1934. Potamogetonaceae. *In* Komarov, V. L., Flora Of The U.S.S.R. Akad. Nauk SSSR: Botanicheskii Institut. Trans. 1968.

ZOLTAI, S. C. 1976. Wetland Classification. Proceedings of the first Meeting on Ecological (Biophysical) Land Classification: 61–71. Petawawa, Ont.

INDEX

Page numbers in bold face refer to the descriptions. Those in italics refer to the illustrations.

Abbreviations ... iv
Acorus ... 18, **98**
calamus ... 14, **98**, *99*
Alisma ... 15, **40**
geyeri ... 41
gramineum ... 13, **41**, 42, 43
plantago ... 41
plantago-aquatica ... **41**, *44*
triviale ... 41
Alismaceae ... 40
Alismataceae ... 13, 14, 15, 18, **40**
Ammannia coccinea ... 18
Anacharis ... 20
canadensis ... 20
nuttallii ... 23
Andromeda polifolia ... 12
Araceae ... 14, 15, 16, 18, **98**
Arales ... 108
Ariflorae ... 108
Arrow-grass ... 48
Arrowhead ... 41
Arum Family ... 98
Arum, yellow ... 101
Azolla ... 13

Balsaminaceae ... 16
Betula ... 12
Betulaceae ... 12
Bidens ... 13, 17
Boraginaceae ... 16
Brasenia ... 16
Bur-reed ... 110
Bur-reed Family ... 110
Butomaceae ... 14, 18, **19**
Butomus ... 18, **19**
umbellatus ... 14, **20**, *21*

Calamus ... 98
Calla ... 14, 16, 18, 19, **98**
palustris ... **98**, *100*
Callitrichaceae ... 18
Callitriche ... 18
Caltha ... 14, 16
Canada Water-weed ... 20
Carex ... 15
Caryophyllaceae ... 17, 18
Cat-tail ... 108
Cat-tail Family ... 108
Ceratophyllaceae ... 12
Ceratophyllum ... 12
Chamaedaphne calyculata ... 12
Chenopodiaceae ... 12, 15
Cicuta ... 13
Compositae ... 13, 14, 17
Cornaceae ... 12
Cornus stolonifera ... 12
Cotula coronopifolia ... 13
Crassulaceae ... 18
Cruciferae ... 13, 14
Cuscuta marina ... 12
Cuscutaceae ... 12
Cyperaceae ... 12, 15, 16

Ditch-grass ... 90
Duck-weed ... 103
Duck-weed Family ... 101
Dulichium arundinaceum ... 15

Eel-grass ... 35, 38
Egeria densa ... 23
Elatinaceae ... 18
Elatine ... 18
Eleocharis ... 12
Elodea ... 16, 19, **20**
canadensis ... **20**, *22*
densa ... **23**, *24*
nuttallii ... **23**, *25*, *26*
Ericaceae ... 12
Eriophorum ... 15
Equisetaceae ... 12
Equisetum ... 12

Fauria crista-galli ... 14
Flowering-rush ... 20
Frog-bit Family ... 20

Gentiana sceptrum ... 17
Gentianaceae ... 13, 14, 17
Geum ... 13
Glaux maritima ... 18
Gramineae ... 15
Grass-wrack ... 35, 38
Gratiola ... 17, 18

Haloragidaceae ... 13
Heteranthera ... 19, **95**
dubia ... 16, **95**, *96*
Hippuridaceae ... 16
Hippuris vulgaris ... 16
Honkenya peploides ... 18
Hydrocharitaceae ... 13, 16, 18, 19, **20**
Hypericaceae ... 17
Hypericum ... 17

Impatiens glandulifera ... 16
Iridaceae ... 15
Iris pseudacorus ... 15
Isoetaceae ... 14
Isoetes ... 14

Jaumea carnosa ... 17
Juncaceae ... 15, 16
Juncaginaceae ... 14, 18, 19, **48**
Juncus ... 16
ensifolius ... 15

Kalmia ... 12

Labiatae ... 13, 17
Ledum ... 12
Lemna ... **103**
minor ... **103**, *104*
trisulca ... **103**, *105*
turionifera ... **103**
Lemnaceae ... 12, 18, **101**
Lentibulariaceae ... 13, 15
Lilaea ... 18, **48**
scilloides ... 14, **48**, *49*
subulata ... 48
Lilaeopsis occidentalis ... 14
Limosella aquatica ... 15
subulata ... 14
Lobelia dortmanna ... 14
Lobeliaceae ... 14
Ludwigia palustris ... 18
Lycopus ... 13, 17
Lysichiton ... 18, **101**
americanum ... 15, **101**, *102*
Lysimachia ciliata ... 18
terrestris ... 17
thyrsiflora ... 17

Lythraceae ... 17, 18
Lythrum salicaria ... 17

Malus diversifolia ... 12
Malvaceae ... 13
Marsilea vestita ... 13
Marsileaceae ... 13
Mentha arvensis ... 17
Menyanthes trifoliata ... 13
Mimulus ... 17
Montia fontana ... 17
Myosotis ... 16
Myrica gale ... 12
Myricaceae ... 12
Myriophyllum ... 13

Naiad ... 92
Naiad Family ... 92
Najadaceae ... 17, 19, **92**
Najas ... 19, **92**
flexilis ... 17, **92**, *94*
Nuphar ... 15
Nymph, water ... 92
Nymphaea ... 15
Nymphaeaceae ... 15, 16

Oenanthe sarmentosa ... 13
Onagraceae ... 18

Pandanaceae ... 108
Pandanales ... 108
Parnassia ... 14, 15
Petasites sagittatus ... 14
Phyllospadix ... 14, 16, **30**
scouleri ... **32**, *33*
serrulatus ... **32**, *34*
torreyi ... **35**, *36*
Pickerel-weed ... 95
Pickerel-weed Family ... 95
Pinguicula ... 15
Polygonaceae ... 16
Polygonum ... 16
Pondweed, alpine ... 56
crisped ... 58
family ... 51
horned ... 90
large-leafed ... 58
sago ... 75
Pondweeds ... 51
Pontederia ... 19, **95**
cordata ... 16, **95**, *97*
Pontederiaceae ... 16, 19, **95**
Portulacaceae ... 17
Potamogeton ... 16, **51**
alpinus ... **56**, *57*
amplifolius ... **58**, *59*
berchtoldii ... 80
compressus ... 65, 88
crispus ... **58**, *60*
diversifolius ... **58**, *61*
epihydrus ... **62**, *63*
filiformis ... **62**, *64*
foliosus ... **65**, *66*
friesii ... **65**, *67*
gramineus ... **68**, *69*
heterophyllus ... 68
hybrids in ... 54
illinoensis ... **68**, *70*
key to species of ... 55
mucronatus ... 65
natans ... **71**, *72*
nodosus ... **71**, 73
okesianus ... **71**, *74*
obtusifolius ... **75**, *76*

Potamogeton—Continued
panormitanus ... 80
pectinatus ... **75**, *77*
perfoliatus ... **75**, *78*, *79*
praelongus ... **80**, *81*
pusillus ... **80**, *82*, *83*
richardsonii ... 75
robbinsii ... **84**, *85*
strictifolius ... **84**, *86*
vaginatus ... **84**, *87*
zosterifolius ... 88
zosteriformis ... **88**, *89*
X *argutulus* ... 55
X *bottnicus* ... 55
X *cognatus* ... 55
X *griffithii* ... 55
X *hagstroemii* ... 55
X *lintonii* ... 55
X *nericeus* ... 55
X *nitens* ... 55
X *olivaceus* ... 55
X *perplexus* ... 55
X *prussicus* ... 55
X *rectifolius* ... 55
X *scoliophyllus* ... 55
X *sparganifolius* ... 55
X *spathulaeformis* ... 55
X *subobtusus* ... 55
X *subsessilis* ... 55
X *suecicus* ... 55
X *undulatus* ... 55
Potamogetonaceae ... 16, 19, **51**
Potentilla palustris ... 13
Primulaceae ... 17, 18

Ranunculaceae ... 13, 14, 15, 16
Ranunculus ... 13
flammula ... 14, 15
Rhynchospora alba ... 16
Rorippa nasturtium-aquaticum ... 13
Rosaceae ... 12, 13
Rotala ramosior ... 18
Ruppia ... **88**
cirrhosa ... 90
maritima ... 16, **90**, *91*
occidentalis ... 90
spiralis ... 90

Sagittaria ... 14, **41**
arifolia ... 45
cuneata ... **45**, *46*
latifolia ... **45**, *47*
Salicaceae ... 12
Salicornia ... 12
Salix ... 12
Salviniaceae ... 13
Sarracenia ... 14
Sarraceniaceae ... 14
Saxifragaceae ... 14, 15
Scheuchzeria ... 19, **30**
Family ... 27
palustris ... 15, 27, **30**, *31*
Scheuchzeriaceae ... 15, 19, **27**
Scirpus ... 15
Scrophulariaceae ... 14, 15, 17, 18
Scutellaria galericulata ... 17
lateriflora ... 17
Sea-grass Family ... 30
Sidalcea hendersonii ... 13
Sisyrinchium californicum ... 15
Sium suave ... 13
Skunk-cabbage ... 101
Sparganiaceae ... 15, 16, 19, **110**

Sparganium ... 15, 16, 19, **110**
americanum ... 110, **111**, *112*
androcladum ... 117
angustifolium ... **111**, *113*, *114*
chlorocarpum ... 111
emersum ... 111
eurycarpum ... **115**, *116*
fluctuans ... **117**, *118*
glomeratum ... **117**, *119*
greenei ... 115, 117
hyperboreum ... **117**, *120*
key to species of ... 110
minimum ... **121**, *122*
multipedunculatum ... 111
simplex ... 111
Spergularia ... 17
Sphagnum ... 27
Spiraea douglasii ... 12
Spirodela ... **106**
polyrhiza ... **106**, *107*
Stachys ... 17
Star-grass, water ... 95
Structures illustrated ... *124*
Suaeda ... 15
Subularia aquatica ... 14
Surf-grass ... 30
Sweetflag ... 98

Tape-grass ... 27
american ... 27
Tillaea aquatica ... 18
Triglochin ... 14, 19, **48**
concinnum ... **48**, *50*
maritimum ... **51**, *52*
palustre ... **51**, *53*
Typha ... 19, **108**
angustifolia ... 4, 108
latifolia ... 15, **108**, *109*
Typhaceae ... 15, 19, **108**

Umbelliferae ... 13, 14
Utricularia ... 13

Vallisneria ... 13, 18, **27**
americana ... **27**, *28*, *29*
spiralis ... 4
Veronica ... 17
Viola palustris ... 14
Violaceae ... 14

Wapato ... 45
Water-meal ... 106
Water-nymph Family ... 92
Water-plantain ... 40
Family ... 40
Water-weed ... 20
Canada ... 20
Nuttall's ... 23
Water Star-grass ... 95
Wolffia ... **106**
borealis ... *104*, **106**
brasiliensis ... 106
punctata ... 106

Zannichellia ... 19, **90**
palustris ... 17, **92**, *93*
Zannichelliaceae ... 17, 19, **90**
Zostera ... 14, 16, **35**
americana ... 35
angustifolia ... 38
hornemanniana ... 38
japonica ... **35**, *37*, 38
marina ... **38**, *39*
minor ... 38
nana ... 38
noltei ... 38
pacifica ... 38
stenophylla ... 38
Zosteraceae ... 13, 14, 16, 18, 19, **30**
Zosterella dubia ... 95

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